A TEXT-BOOK

OF

HUMAN PHYSIOLOGY.

A TEXT-BOOK OF HUMAN PHYSIOLOGY,

INCLUDING

HISTOLOGY AND MICROSCOPICAL ANATOMY;

WITH SPECIAL REFERENCE TO THE REQUIREMENTS OF

PRACTICAL MEDICINE.

BY

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TRANSLATED FROM THE SEVENTH GERMAN EDITION.

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[The illustrations indicated by the word *Hermann* are from Hermann's *Handbuch der Physiologie;* by *Cadiat*, from Cadiat's *Traité d'Anatomie Générale;* by *Ranvier*, from Ranvier's *Traité Technique d'Histologie;* by *Brunton*, from Brunton's *Text-book of Pharmacology, Therapeutics, and Materia Medica;* by *Schenk*, from Schenk's *Grundriss der normalen Histologie;* by *Ecker*, from Ecker's *Anatomie des Frosches*, 2nd ed.; by *Quain*, from *Quain's Anatomy;* by *Stöhr*, from Stöhr's *Lehrbuch der Histologie*, Jena, 1887; by *Obersteiner*, from H. Obersteiner's *Anleitung beim Studium des Baues der nervösen Centralorgane*, Wien, 1888; by *Jolyet* from Viault and Jolyet's *Traité de Physiologie*, 1889; by *Renaut*, from *Traite d'histologie pratique*, Paris, 1889.]

Physiology of the Motor Apparatus.

291. [**CILIARY MOTION—PIGMENT CELLS.**—(*a*) **Muscular Movement.**—By far the greatest number of the movements occurring in our bodies is accomplished through the agency of **muscular fibre**, which, when it is excited by a stimulus, contracts, *i.e.*, it forcibly shortens, and thus brings its two ends nearer together, while it bulges to a corresponding extent laterally. In muscle the contraction takes place in a **definite direction.**]

[(*b*) **Amœboid Movement.**—Motion is also exhibited by colourless blood-corpuscles, lymph-corpuscles, leucocytes, and some other corpuscles. In these structures we have examples of amœboid movement (§ 9), which is movement in an **indefinite direction.**]

[(*c*) **Ciliary Movement.**—There is also a peculiar form of movement, known as *ciliary movement.* There is a gradual transition between these different forms of movement. The **cilia** which are attached to the ciliated epithelium are the motor agents (fig. 364).]

[**Ciliated epithelium—where found.**—In the nasal mucous membrane, except the olfactory region; the cavities accessory to the nose; the upper half of the pharynx, Eustachian tube, larynx, trachea, and bronchi; in the uterus, except the lower half of the cervix; Fallopian tubes; vasa efferentia to the lower end of epididymis; ventricles of brain (child); and the central canal of the spinal cord.]

[The **cilia** are flattened blade-like or hair-like appendages attached to the free end of the cells. They are about $\frac{1}{3000}$ inch in length, and are apparently homogeneous and structureless. They are planted upon a clear non-contractile **disc** on the free end of the cell, and some observers state that they pass through the disc to become continuous with the protoplasm of the cell, or with the plexus of fibrils which pervades the protoplasm, so that by some observers they are regarded as prolongations of the intra-epithelial plexus of fibrils. They are specially modified parts of an epithelial cell, and are contractile and elastic. They are colourless, tolerably strong, not tinged by staining reagents, and are possessed of considerable rigidity and flexibility. They are always connected with the protoplasm of cells, and are never outgrowths of the solid cell membranes. There may be 10 to 20 cilia distributed uniformly on the free surface of a cell (fig. 364).]

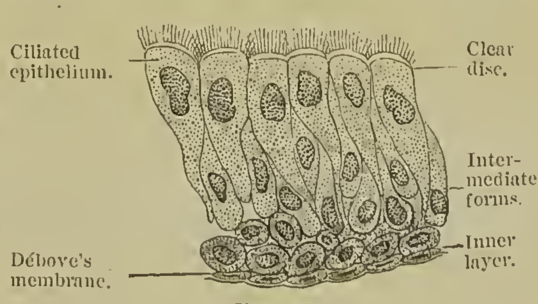


Fig. 364.
Ciliated epithelium.

[In the large ciliated cells in the intestine of some **molluscs** (mussel), the cilia perforate the clear refractile disc, which appears to consist of small globules—**basal pieces**—united by their edge, so that a cilium seems to spring from each of these, while continued downwards into the protoplasm of the cell, but not attached to the nucleus, there is a single varicose fibril—**rootlet**,

and the leash of these fibrils passes through the substance of the cell and may unite towards its lower tailed extremity (*Engelmann*).]

Ciliary motion may be studied in the gill of a mussel, a small part of the gill being teased in *sea water*; or the hard palate and œsophagus of a frog, newly killed, may be scraped and the scraping examined in ¾ p.c. salt solution. The whole of the mucous membrane of the frog's palate and œsophagus may be examined. In this case the particles moved by the cilia are carried towards the stomach. On analysing the movement, all the cilia will be observed to execute a regular, periodic, to and fro rhythmical movement in a plane usually vertical to the surface of the cells, the direction of the movement being parallel to the long axis of the organ. The appearance presented by the movements of the cilia is sometimes described as a lashing movement, or like a field of corn moved by the wind. Each **vibration** of a cilium consists of a rapid forward movement or flexion, the tip moving more than the base, and a slower backward movement, the cilium again straightening itself. The forward movement is at least twice as rapid as the backward movement. The **amplitude** of the movement varies according to the kind of cell and other conditions, being less when the cells are about to die, but it is the same for all the cilia attached to one cell, and is seldom more than 20° to 50°. There is a certain **periodicity** in their movement—in the frog they contract about 12 times per second. The result of the rapid forward movement is that the surrounding fluid, and any particles it may contain, are moved in the direction in which the cilia bend. All the cilia of adjoining cells do not move at once, but in regular succession, the movement travelling from one cell to the other, but how this **co-ordination** is brought about we do not know. At least it is quite independent of the nervous system, as ciliary movement goes on in isolated cells, and in man it has been observed in the trachea two days after death. [Kraft has shown, in the case of the frog, that when the ciliated cells of the palate are stimulated mechanically the condition of excitation is more readily propagated in a longitudinal direction towards the stomach than laterally or towards the mouth, so that its excitability to mechanical stimuli is most marked in the direction of its physiological activity. The co-ordination seems to depend on the transference of the condition of excitement of the cells, in this case from higher to lower placed cells.]

[**Conditions for Ciliary Movement.**—In order that ciliary movement may go on, it is essential that (1) the cilia be connected with part of a cell; (2) moisture; (3) oxygen be present; and (4) the temperature be within certain limits.]

[A ciliated epithelial cell is a good example of the **physiological division of labour.** It is derived from a cell which originally held motor, automatic, and nutritive functions all combined in one mass of protoplasm; but in the fully developed cell, the nutritive and regulative functions are confined to the protoplasm, while the cilia alone are contractile. If the cilia be separated from the cell, they no longer move. If, however, a cell be divided so that part of it remains attached to the cilia, the latter still move. The nucleus is not essential for this act. It would seem, therefore, that though the cilia are contractile, the motor impulse probably proceeds from the cell. Each cell can regulate its own nutrition, for during life they resist the entrance of certain coloured fluids.]

[**Effect of Reagents on Ciliary Motion.**—Gentle **heat** accelerates the number and intensity of the movements, **cold** retards them. A temperature of 45° C. causes coagulation of their proteids, makes them permanently rigid, and kills them, just in the same way as it acts on muscle, causing heat-stiffening (§ 295, 1). **Weak alkalies** may cause them to contract after their movement is arrested or nearly so (*Virchow*), and any current of fluid in fact may do so. Cilia after being in action for a time show signs of fatigue like muscle. It may be, as in muscle, acid proteids are formed, and that the weak alkali neutralises the acid fatigue-products. Lister showed that the vapour of **ether** and **chloroform** arrests the movements as long as the narcosis lasts, but if the vapour be not applied for too long a time, the cilia may begin to move again. The prolonged action of the

vapour kills them. As yet we do not know any specific poison for cilia—atropin, veratrin, and curare acting like other substances with the same endosmotic equivalent (*Engelmann*). Electrical stimulation seems to act simultaneously at both poles (*Kraft*).]

[**Functions of Cilia.**—The moving cilia propel fluids or particles along the passages which they line. By carrying secretions along the tubes which they line towards where these tubes open on the surface, they aid in **excretion.** In the respiratory passages, they carry outwards, along the bronchi and trachea, the mucus formed by the mucous glands in these regions. When the mucus reaches the larynx it is either swallowed or coughed up. That the cilia carry particles upwards in a spiral direction in the trachea has been proved by actual laryngoscopic investigation, and also by excising a trachea and sprinkling a coloured powder on its mucous membrane, when the coloured particles (Berlin blue or charcoal) are slowly carried towards the upper end of the trachea. In bronchitis the ciliated epithelium is shed, and hence the mucus tends to accumulate in the bronchi. They remove mucus from cavities accessory to the nose, and from the tympanum, while the ova are carried partly by their agency from the ovary along the Fallopian tube to the uterus. In some of the lower animals, they act as organs of locomotion, and in others as adjuvants to respiration, by creating currents of water in the region of the organs of respiration.

[**The Force of Ciliary Movement.**—Wyman and Bowditch found that the amount of work that can be done by cilia is very considerable. The work was estimated by the weight which a measured surface of the mucous membrane of the frog's hard palate was able to carry up an inclined plane of a definite slope in a given time.]

[**Pigment-cells** belong to the group of contractile tissues, and are well developed in the frog, and many other animals where their characters have been carefully studied. They are generally regarded as comparable to branched connective-tissue corpuscles, loaded with pigmented granules of **melanin.** The pigment-granules may be diffused in the cell, or aggregated around the nucleus; in the former case, the skin of the frog appears dark in colour; in the latter, it is but slightly pigmented (fig. 365).]

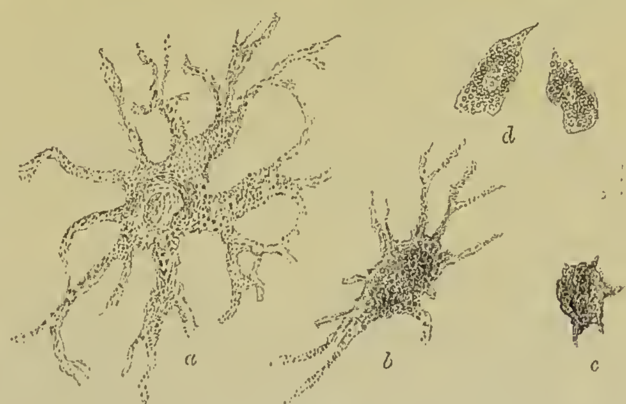


Fig. 365.

Pigment-cells from the web of frog's foot; *a*, cell with pigment-granules diffused; *b*, granules more concentrated; *c*, more concentrated still; *d*, cells with guanin-granules (*Stirling*).

Conditions affecting frog's pigment-cells.— They undergo marked changes of shape under various influences. If the motor-nerve to one leg of a frog be divided, the skin of the leg on that side becomes gradually darker in colour than the intact leg. A similar result is seen in the curare experiment, when all parts are ligatured except the nerve. Local applications affect the state of diffusion of the pigment, as v. Wittich found that turpentine or electricity caused the cells of the tree-frog to contract, and the same effect is produced by light. In Rana temporaria local irritation has little effect, but light, on the contrary, has, although the effect of **light** seems to be brought about through the eye, probably by a reflex mechanism (*Lister*). A pale-coloured frog, put in a dark place, assumes, after a time, a different colour, as the pigment is diffused in the dark; but if it be exposed to a bright light it soon becomes pale again. The same phenomenon may be seen

on studying the web of a frog's leg under the microscope. The marked variations of colour—within a certain range—in the chameleon is due to the condition of the pigment-cells in its skin, covered as they are by epidermis, containing a thin stratum of air (*Brücke*). When it is poisoned with strychnin, its whole body turns pale; if it be ill, its body becomes spotted in a dendritic fashion, and if its cutaneous nerves be divided, the area supplied by the nerve changes to black. The condition of its skin, therefore, is readily affected by the condition of its nervous system, for psychical excitement also alters its colour. If the sympathetic nerve in the neck of a turbot be divided, the skin on the dorsal part of the head becomes black. It is well known that the colour of fishes is adapted to the colour of their environment. If the nerve proceeding from the stellate ganglion in the mantle of a cuttle-fish be divided, the skin on one half of the body becomes pale. The intra-epithelial pigment-cells of the membrane lining the abdomen and those of the tail in the salamander undergo division by mitosis. At first the processes of the branched cell are retracted, the nucleus divides by mitosis, but at first the pigment is in the protoplasm outside the chromatin figure, but later it lies between the chromatin loops, while in the dyaster stage it is all accumulated at the equator, but none occurs within the chromatin figures (*Waldeyer*, *Zimmermann*).]

[**Guanin in Cells.**—Besides the pigment-cells in the web of a frog's foot (especially in Rana temporaria) there are other cells which contain granules of guanin (fig. 365, *d*). If the web of a frog's foot be mounted in Canada balsam and examined microscopically between crossed Nicol's prisms, each guanin-cell is seen to contain numerons very strongly doubly refractive granules of guanin (§ 283).]

292. STRUCTURE AND ARRANGEMENT OF MUSCLES.—[**Muscular Tissue** is endowed with **contractility**, so that when it is acted upon by certain forms of energy or stimuli, it contracts. There are two varieties of this tissue—

(1) **Striped**, striated (or voluntary);
(2) **Non-striped**, smooth, organic (or involuntary).

Some muscles are completely under the control of the will, and are hence called "**voluntary**," and others are not directly subject to the control of the will, and are hence called "**involuntary**;" the former are for the most part striped, and the latter non-striped; but the heart-muscle, although striped, is an involuntary muscle.]

1. **Striped Muscles.**—The surface of a muscle is covered with a connective-tissue envelope or **perimysium externum**, from which septa, carrying blood-vessels and nerves, the **perimysium internum**, pass into the substance of the muscle, so as to divide it into bundles of fibres or **fasciculi**, which are fine in the eye-muscles and coarse in the glutei. In each such compartment or mesh there lie a number of *muscular fibres* arranged more or less parallel to each other. [The fibres are held together by delicate connective-tissue or **endomysium**, which surrounds groups of the fibres; each fibre being, as it were, separated from its neighbour by delicate fibrillar connective-tissue.] Each muscular fibre is surrounded with a rich plexus of *capillaries* [which form an elongated meshwork, lying between adjacent fibres, but never penetrating the fibres, which, however, they cross (fig. 371). In a contracted muscle, the capillaries may be slightly sinuous in their course, but when a muscle is on the stretch these curves disappear. The capillaries lie in the endomysium, and near them are *lymphatics*]. Each muscular fibre receives a nerve-fibre. [**Where found.**—Striped muscular fibres occur in the skeletal muscles, heart, diaphragm, pharynx, upper part of œsophagus, muscles of the middle ear and pinna, the true sphincter of the urethra, and external anal sphincter.]

A muscular fibre (fig. 366, 1) is a more or less cylindrical or polygonal fibre, 11 to 67 μ [$\frac{1}{2300}$ to $\frac{1}{400}$ in.] in diameter, and never longer than 3 to 4 centimetres [1 to $1\frac{1}{4}$ in.]. Within short muscles, *e.g.*, stapedius, tensor tympani, or the short

muscles of a frog, the fibres are as long as the muscle itself; within longer muscles, however, the individual fibres are pointed, and are united obliquely by cement-substance with a similar bevelled or pointed end of another fibre lying in the same direction. Muscular fibres may be isolated by maceration in nitric acid with excess of potassic chlorate or by a 35 per cent. solution of caustic potash.

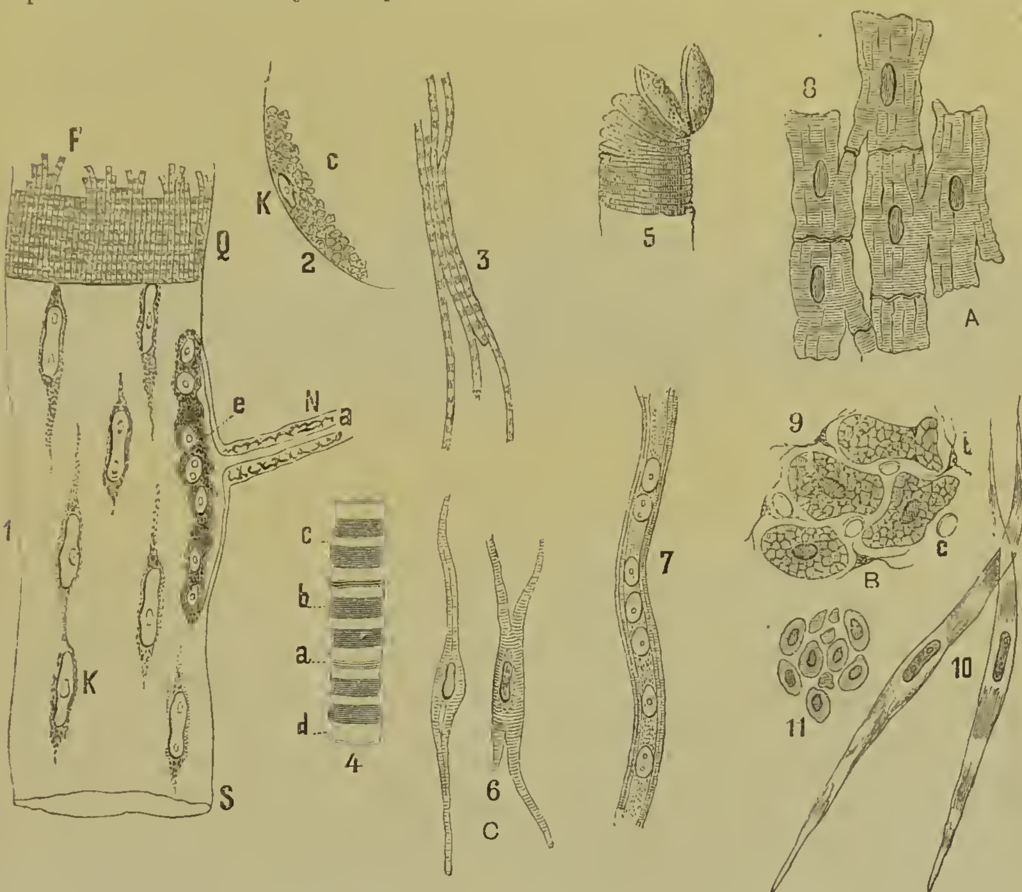


Fig. 366.

Histology of muscular tissue. 1. Diagram of part of a striped muscular fibre; S, sarcolemma; Q, transverse stripes; F, fibrillæ; K, the muscle-nuclei; N, a nerve-fibre entering it with *a*, its axis cylinder and Kühne's motorial end-plate, *c*, seen in profile; 2, transverse section of part of a muscular fibre, showing Cohnheim's areas, *c*; 3, isolated muscular fibrillæ; 4, part of an insect's muscle greatly magnified; *a*, Krause-Amici's line limiting the muscular cases; *b*, the doubly-refractive substance; *c*, Hensen's disc; *d*, the singly-refractive substance; 5, fibres cleaving transversely into discs; 6, muscular fibre from the heart of a frog; 7, development of a striped muscle from a human fœtus at the third month; 8, 9, muscular fibres of the heart; *c*, capillaries; *b*, connective-tissue corpuscles; 10, smooth muscular fibres; 11, transverse section of smooth muscular fibres.

[Each muscular fibre consists of the following parts:—

1. **Sarcolemma** or **myolemma**, an elastic sheath, enclosing the sarcous substance;
2. The included **sarcous substance**;
3. The **nuclei** or muscle-corpuscles.]

Sarcolemma.—Each muscular fibre is completely enclosed by a thin colourless, structureless, transparent elastic sheath (fig. 366, 1, S)—the **sarcolemma**—which, chemically, is mid-way between connective and elastic tissue, and within it is the contractile substance of the muscle. [When a muscular fibre is being digested by trypsin, Chittenden observed, at the beginning, the sarcolemma raised from its

sarcous contents as a folded tube, but it is ultimately digested by trypsin. It is thus distinguished from the collagen substance of connective-tissue, which is not digested by trypsin. It is not dissolved by boiling, and it resists the action of acids and dilute alkalies, while it is dissolved by concentrated alkalies. Thus, it differs from elastic fibres, and on the whole, chemically, it seems to be most closely related to the membrana propria of glands. It has much more cohesion than the sarcous substance which it encloses, so that sometimes, when teasing fresh muscular tissue under the microscope, one may observe the sarcous substance torn across, with the unruptured sarcolemma stretching between the ends of the ruptured sarcous substance. If muscular fibres be teased in distilled water, sometimes fine clear blebs are seen along the course of the fibre, due to the sarcolemma being raised by the fluid diffusing under it. The sarcous substance, but not the sarcolemma, may be torn across by plunging a muscle in water at 55° C., and keeping it there for some time (*Ranvier*).]

[In the frog there is an exceedingly thin membrane covering the retro-lingual lymph-sac. Ranvier calls this the **retro-lingual membrane**, and it contains isolated branched striped muscular fibres. He finds that the sarcolemma has elastic fibres directly continuous not only with its terminations, but also with its margins. Thus the one is attached to the other, the elastic fibre being cemented as it were to the sarcolemma. The elastic fibres are deeply stained by methyl-violet, the sarcolemma but slightly. He also finds that the sarcous matter ends in a broad dim anisotropous disc.]

Sarcous Substance.—The sarcous substance is marked transversely by alternate light and dim layers, bands, **stripes** or **discs** (fig. 366, 1, Q), so that each fibre is said to be "**transversely striped.**" [The stripes do not occur in the sarcolemma, but are confined to the sarcous substance, and they involve its whole thickness.]

[The animals most suited for studying the structure of the sarcous substance are some of the insects. The muscles of the water-beetle, Dytiscus marginalis, and the Hydrophilus piceus are well suited for this purpose. So is the crab's muscle. In examining a living muscle microscopically, no fluid except the muscle-juice should be added to the preparation, and very high powers of the microscope are required to make out the finer details.]

Bowman's Discs.—If a muscular fibre be subjected to the action of hydrochloric acid (1 per 1000), or if it be digested by gastric juice, or if it be frozen, it tends to cleave transversely into **discs** (*Bowman*), which are artificial products, and resemble a pile of coins which has been knocked over (fig. 366, 5).

Fibrillæ.—Under certain circumstances a fibre may exhibit *longitudinal striation*. This is due to the fact that it may be split up longitudinally into an immense number of (1 to 1·7 μ in diameter) fine, contractile threads, the **primitive fibrillæ** (fig. 366, 1, F), placed side by side, each of which is also transversely striped, and they are so united to each other by semi-fluid cement-substance that the transverse markings of all the fibrillæ lie at the same level. Several of these fibrils are united together owing to the mutual pressure, and prismatic in form, so that when a transverse section of a perfectly fresh muscular fibre is observed after it is frozen, the end of each fibre is mapped out into a number of small polygonal areas called **Cohnheim's areas** (fig. 366, 2). [Each bundle of fibrils or polygonal area represents what Kölliker called a "**Muscle-Column.**"]

Fibrillæ are easily obtained from insects' muscles, while those from a mammal's muscle are readily isolated by the action of dilute alcohol, Müller's fluid [or, best of all, $\frac{1}{6}$ per cent. solution of chromic acid] (fig. 366, 3).

[In studying the structure of muscle, it is well to remember that there are considerable differences between the muscles of Vertebrates and those of Arthropoda.]

[When a **living** unaltered **vertebrate muscular fibre** is examined microscopically, in its own juice, we observe the alternate dim and light transverse discs. Amici, Krause, and Dobie showed that a fine dark line runs across the light disc, and divides it into two (fig. 367). This line has been called **Dobie's line** or **intermediate line.** Amici resolved it into a row of granules, and by others (*e.g.*,

Krause) it is regarded as due to the existence of a membrane,—hence it is called **Krause's membrane**,—which runs transversely across the fibre, being attached all round to the sarcolemma, thus dividing each fibre into a series of *compartments* placed end to end. Hensen described a disc or stripe in the centre of the dim disc.]

[On **Krause's theory** each **muscular compartment** contains (1) a **broad dim disc**, which is the *contractile* part of the sarcous substance. It is doubly refractive (**anisotropous**), and is composed of Bowman's sarcous elements. (2) On each end of this disc, and between it and Krause's membranes, is a narrower, clear, homogeneous, and but singly refractile (**isotropous**), soft or fluid substance, which forms the **lateral disc** of Engelmann. In some insects it contains a row of refractive granules, constituting the **granular layer** of Flögel. If a muscular fibre be stretched and stained with logwood, the central part of the dim disc appears lighter in colour than the two ends of the same disc. This has been described as a separate disc, and is called the **median disc** of Hensen (fig. 366, 4, *c*).

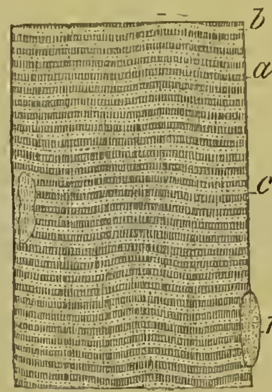


Fig. 367.

Muscular fibre of a rabbit. *a*, disc.; *b*, light disc; *c*, intermediate or Dobie's line ; *n*, nucleus seen in profile.

[In an unaltered fibre, the dim broad stripe may appear homogeneous, but after a time it cleaves throughout its entire extent in the long axis of the fibre into a number of prismatic elements of fibrils, the **sarcous elements** of Bowman (fig. 366). These at first are prismatic, but as they solidify they shrink and seem to squeeze out of them a fluid, becoming at the same time more constricted in the centre. This separation into bundles of fibrils with an interstitial matter gives rise to the appearance seen on transverse section of a frozen muscle, and known as Cohnheim's areas (fig. 366, 2, *c*). In all probability the cleavage also extends through the lateral discs, and thus fibrils are formed by longitudinal cleavage of the fibre.]

[**Muscles of Arthropoda.**—Engelmann showed that the muscles of these animals have a large number of discs. In a muscle of an animal killed by being plunged into alcohol, according to the position of the lens of the microscope, one sees—

1. The broad dim disc, composed of two darker lateral portions or discs, and a lighter disc—that of Hensen, between them. In fig. 368 the whole disc is marked Q, and Hensen's disc is distinguished as *h*.
2. On both sides of this is a small, clear, slightly refractive stripe, J, corresponding to one of Engelmann's isotropous stripes.
3. On both sides there follows symmetrically a dark strongly refractive stripe, N, corresponding to Engelmann's accessory stripe and Flögel's granular layer.
4. Then on both sides there is a clear, feebly refractive disc, E.
5. Beyond E is a small dark, highly refractive stripe, Z—usually the darkest—corresponding to the Amici-Krause line.]

[From Z the stripes are repeated in the inverse order to Q, then in the same order to Z, and so on. This is the appearance with a low position of the lens. Many muscles do not show all these stripes, thus *h* is often absent.]

[If the lens of the microscope be raised, to get a more superficial view of the fibre, the distribution of the light is reversed (fig. 368, II), as all strongly refractive sections become light and all feebly refractive appear darker, while with a deep position of the lens, the reverse is the case.]

[Experiment shows that the dim disc rapidly swells up in dilute acids, and also that the dim discs (Q), the accessory discs (N), and the Amici-Krause line (K), stain more deeply with logwood than the other discs, and *h* less than the rest of Q.]

[If a muscle which has been some time in alcohol be examined as to its **longitudinal striation**, it will be seen to consist of rods with light intervals between them (fig. 369). The rods are thicker at their ends, and thinner and lighter at their middle. Rollett regards the clear intervals between these rods as consisting of **sarcoplasma**, a body closely related to protoplasm, and the rods as bundles of fibrillæ or "muscle-columns."]

[If a muscle be acted upon by certain acids the relative appearance of the muscle-columns and the sarcoplasma is altered ; and the latter may appear in these and in gold preparations as a plexus of fibrils with regular longitudinal and transverse meshes (*Melland*, *Marshall*, fig. 370.

Muscle-Rods.—Schäfer describes the appearance differently :—Double rows of granules are

seen lying in or at the boundaries of the light streaks (discs), and very fine longitudinal lines may be detected running through the dark streak (dim disc) and uniting the minute granules. These fine lines, with their enlarged extremities, are "**muscle-rods.**" They are most conspicuous in insects. During the contraction of a living muscular fibre, Schäfer describes the "reversal of the stripes" (§ 297) as follows:—"When the fibres contract, the light stripes are seen, as the fibres shorten and thicken, to become dark, an apparent reversal being thereby produced in the striæ. This reversal is due to the enlargement of the rows of dark dots and the formation by their juxtaposition and blending of dark discs, whilst the muscular substance between these discs has by contrast a bright appearance." With **polarised light** in a living muscular fibre, all the sarcous substance, except the muscle-rod, is doubly refractive or anisotropous, so that it appears bright on a dark field when the Nicol's prisms are crossed, while under the same conditions contracted muscle and dead muscle show alternate dark and light bands (*Schäfer*).]

The **nuclei** or **muscle-corpuscles** are found immediately under the sarcolemma in all mammals, and their long axis lies in the long axis of the fibre (8 to 13 μ long, 3 to 4 μ broad).

[In the muscles of the frog, reptiles, and some other animals, *e.g.*, the red muscles of the rabbit and hare and in some muscles of birds, they lie in the substance of the fibre surrounded by a small amount of protoplasm.] When they occur immediately under the sarcolemma they are more or less flattened, and lie embedded in a small amount of protoplasm (fig. 366, 1 and 2, K). They contain one or two nucleoli, and it is said that the protoplasm sends out fine processes which unite with similar processes from adjoining corpuscles, so that, according to this view, a branched protoplasmic network exists under the sarcolemma. [Each nucleus has a reticulated appearance due to the presence of a plexus of fibrils, consisting of chromatin; in its meshes lies an achromatic substance. The nuclei are specially large in Otiorhynchus planatus, one of the beetles. Mitotic figures indicating division of the nuclei have been observed. The nuclei are not seen in a perfectly fresh muscle, because, until they have undergone some change, their refractive index is the same as that of the sarcous substance.] They become specially evident after the addition of acetic acid. Histogenetically, they are the remainder of the cells from which the muscular fibres were developed (fig. 366, 7). According to M. Schultze, the sarcous substance is an intercellular substance differentiated and formed by their activity. Perhaps they are the centres of nutrition for the muscular fibres. In amphibians, birds, fishes, and reptiles, they lie in the axis of the fibres between the fibrils.

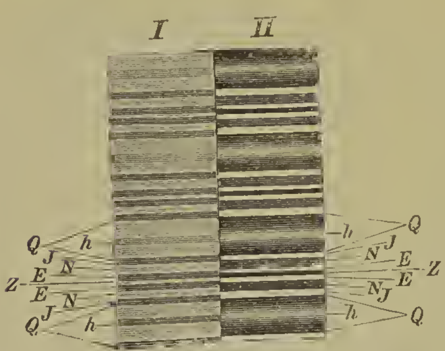


Fig. 368.

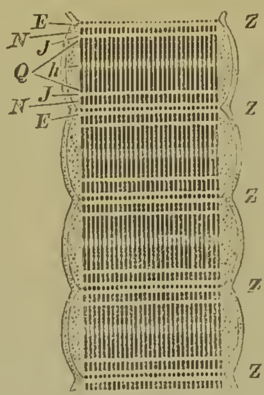


Fig. 369.

Fig. 368.—Insects' muscle; I, with a high position of the lens, and II with a deeper position. Fig. 369.—Muscular fibre of Carabus cancellatus.

Sarcoplasma.—It is said that the protoplasm of the muscle-corpuscles forms a fine network throughout the whole muscular fibre, the transverse branches taking the course of the intermediate or Dobie's, line and the longitudinal branches running in the interstices between Cohnheim's areas, constituting the sarcoplasma (*Retzius, Bremer, Melland*, fig. 370).

Relation to Tendons.—According to Toldt, the delicate connective-tissue elements, which cover the several muscular fibres, pass from the ends of the latter directly into the connective-tissue elements of the tendon. The end of the muscular fibre is perhaps united to the smooth surface or hollow end of the tendon by means of a special cement (*Weismann*—fig. 371, S). In arthropoda, the sarcolemma passes directly into and becomes continuous with the tendon (*Leydig*). The tendon itself consists of longitudinally arranged bundles of white fibrous tissue with cells—*tendon cells*—embracing them (p. 573). There is a loose capsule or sheath of connective-tissue—the **peritendineum** of Kollman—surrounding the

whole and carrying the blood-vessels, lymphatics, and nerves. The tendons move in the tendon-sheaths, which are moistened by a mucous fluid. In most situations, muscular fibres are attached by means of tendons to some fixed point, but in other situations (face) the ends terminate between the connective-tissue elements of the skin. [Relation to elastic fibres, p. 564.]

[**Blood-Vessels of Muscle.**—Muscles, being very active organs, are richly supplied with blood. The blood-supply of a muscle differs from some organs in not constituting an actual vascular unit, supplied only by one artery and one vein, thus being unlike the kidney, spleen, &c. Each muscle usually receives *several* branches from different arteries, and branches enter it at certain distances along its whole length. The artery and vein usually lie together in the connective-tissue of the perimysium, while the capillaries lie in the endomysium. The capillaries lie between the muscular fibres, but **outside the sarcolemma**, where they form an elongated rich plexus with numerous transverse branches (fig. 372). The lymph to nourish the sarcous substance must traverse the sarcolemma to reach the former. In the **red muscles** of the rabbit (*e.g.*, semitendinosus) the capillaries are more wavy, while on the transverse

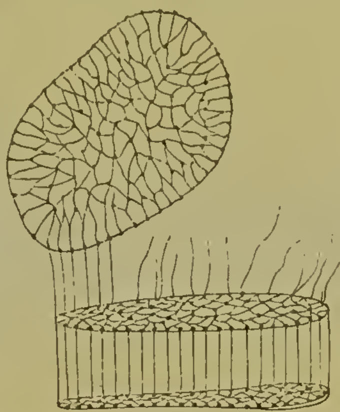


Fig. 370.

Fig. 371.

Fig. 370.—Network in a muscular fibre. Fig. 371.—Relation of a tendon, S, to its muscular fibre.

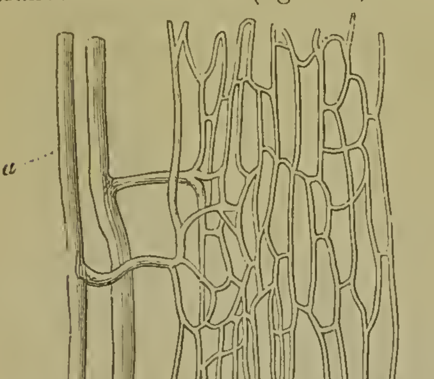


Fig. 372.

Fig. 373.

Fig. 372.—Injected blood-vessels of a human muscle. *a*, small artery ; *b*, vein ; *c*, capillaries. × 250. Fig. 373.—Blood-vessels of a rabbit's red muscle injected ; A, artery ; V, veins; *n*, dilatations on the transverse branch of the capillaries ; *m*, position of the muscular fibres which are omitted ; *s*, longitudinal sinuous branches.

branches of some of the capillaries, and on the veins, there are small, oval, saccular dilatations (fig. 373), which act as reservoirs for blood (*Ranvier*).]

[Spalteholz finds that the arteries form a close plexus in muscle, with quadrangular meshes, the long axis being in the direction of the fibres. From this fine arteries proceed at right angles to break up into capillaries. In a **relaxed muscle** the capillaries are extended, but in a **contracted muscle** they are more or less curved. The veins run along with the arteries, and are provided with valves even to their finest branches. Each muscle is to be regarded as a closed system for its blood-stream. There is so free an anastomosis in muscle as to permit of a free distribution of blood to all its parts, while the venous system is so arranged that the products of muscular metabolism are carried out of the muscle as quickly and completely as possible.]

[**Lymphatics.**—We know very little of the lymphatics of muscle, although the lymphatics of tendon and fascia have been carefully studied by Ludwig and Schweigger-Seidel. There are lymphatics in the endomysium of the heart, which are continuous with those under the pericardium. This subject still requires further investigation. Compare the lymphatics of the fascia lata of the dog (fig. 278, § 201).]

Entrance of the Nerve.—The *trunk* of the motor nerve, as a rule, enters the muscle at its geometrical centre (*Schwalbe*); hence, the point of entrance in muscles with long, parallel, or spindle-shaped fibres lies near its middle. If the muscle with parallel fibres is more than 2 to 8 centimetres [1–3 inches] in length, several branches enter its middle. In triangular muscles, the point of entrance of the nerve is displaced more towards the strong tendinous point of convergence of the muscular fibres. A nerve-fibre usually enters a muscle at the point where there is the least displacement of the muscular substance during contraction.

Motor Nerve to Muscle.—Every muscle-fibre receives a motor nerve-fibre (fig. 366, 1, N). Each nerve does not contain originally as many motor nerve-fibres as there are muscular fibres in the muscle it enters; in the human eye-muscles, there are only 3 nerve-fibres to 7 muscular fibres; in other muscles (dog), 1 nerve-fibre to 40 or 80 (*Tergast*). Hence, when a nerve enters a muscle it must divide, which occurs dichotomously [at Ranvier's nodes], the structure undergoing no change until there are exactly as many nerve-fibres as muscular fibres. In warm-blooded animals each muscular fibre has only one, while cold-blooded animals have several points of insertion of the nerve-fibre (*Sandmann*). A nerve-fibre enters each muscular fibre, and where it enters it forms an eminence (*Doyère*, 1840), the **eminence of Doyère**, or "**motorial end-plate**" or "**motor spray**" of Kühne (figs. 366, 1, *e*, 374, 375, 376, 377).

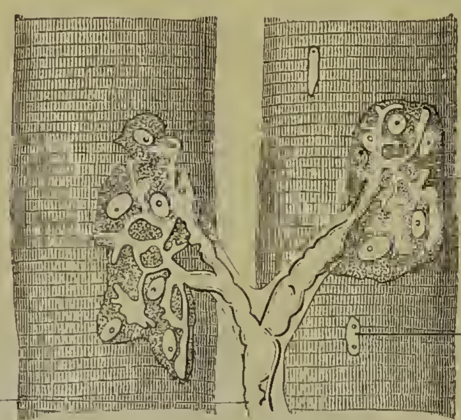


Fig. 374.
Muscular fibres with motorial end-plates.

[The elaborate investigations of K. Mays on the exact distribution of nerve-fibres in the muscles of the frog have conclusively proved—apart from experimental reasons—that parts of muscles receive no nerve-fibres at all, certain portions being free from nerves, *e.g.*, the terminal portions of the sartorius muscle of the frog. This has been proved for all classes of vertebrates except osseous fishes.]

[The mode of termination of a motor nerve in a muscular fibre is not the same in all animals, but in every case it pierces the sarcolemma, and its ultimate distribution has a distinct hypolemmal character. The Doyère's eminence is present in most mammals and reptiles, but in amphibians and birds the ending is flat on the muscle-fibre. Most of the results known to us have been worked out by Kühne. The nerve-endings, then, are confined to very small spots or areas on the muscular fibres, termed by Kühne "**fields of innervation.**" Most nerve-fibres

have only one such field but very long fibres may have, at most, eight. One or more medullated nerve-fibres pass—as preterminal or epilemmal fibres—from the point of division of the nerve-fibre to the muscular fibre, to pass into the nerve-endings. The nerve-endings consist of divisions of the axial cylinder, which are distributed over the sarcous substance without (so far as is known) forming any direct connection with it. The endings, however, lie in direct contact with it. This branched arrangement of the axis-cylinder under the sarcolemma Kühne has called a "**motor-spray**" ("motorisches Geweih"), and the mode of distribution of the branches varies in different classes of animals. In the frog (fig. 376), tailed amphibians, and birds, the hypolemmal branches of the axis-cylinder form bayonet-like and branched endings. In the lizard, snakes, and mammals, the branches are often curved or twisted, and possessed of lobes, and as the division is very variable, there is every form from a simple hook-like bend to a highly arborescent termination (fig. 375).]

[Where a motor nerve enters a muscular fibre at the eminence of Doyère, the sheath of the nerve-fibre, known as the perineural or Henle's sheath (§ 321),

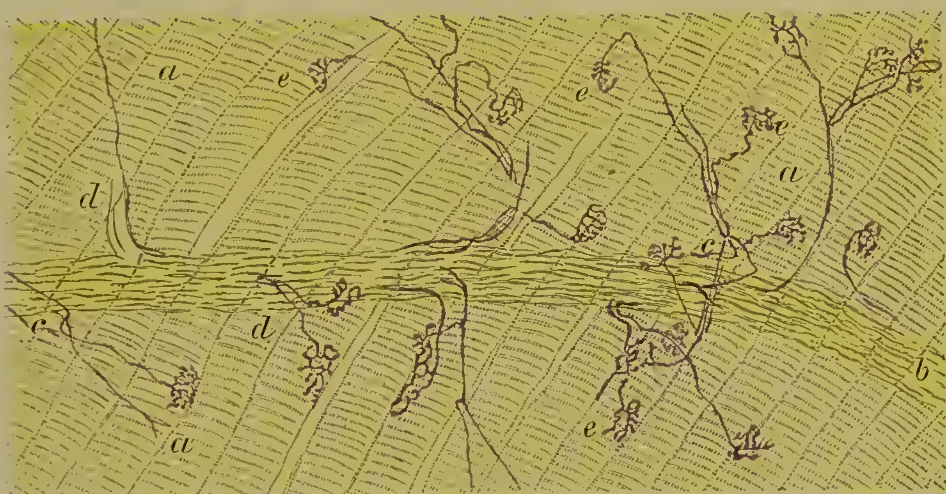


Fig. 375.

Motor terminations in a lizard, stained by methylene blue. *a*, muscular fibres; *b*, a nerve trunk, which splits up into small branches, *c*, containing a few medullated fibres, *d*. The medullated fibres, *d*, end in motorial end-plates, *e*.

becomes continuous with the sarcolemma. The eminence itself consists of a mass of protoplasm—or sarcoplasm—called by Kühne **sarcoglia**—which contains granules and nuclei, the latter with a membrane and peculiar nucleoli; the nuclei themselves are the fundamental or basal nuclei of the sarcoglia. The outer surface of the eminence is covered by a membrane called **telolemma** by Kühne, but which in reality consists of two membranes, an outer one, the **epilemma**, continuous with the perineural or Henle's sheath, and an inner one, the **endolemma**, the continuation of the sheath of Schwann of the nerve-fibre, both ultimately being connected with the sarcolemma. As the nerve pierces the muscular fibre, it loses its myelin, and with it disappears the keratin sheath or axilemma of the axis-cylinder, so that the spray-like ending is accompanied only by the telolemma (fig. 377). The telolemma contains nuclei which are derived from Henle's sheath (*Kühne*).]

[In some animals, such as the lizard, in order to see the nerve-terminations, it is sufficient to stain portions of fresh muscles with Delafield's logwood or to inject methylene blue into the blood (fig. 375).]

[Nerve-endings, then, are sublemmar, and the terminations of the nerves never penetrate into the depth of the muscular fibre, but come into direct contact with the contractile prism or cylinder moistened by the fluids of the muscle. In many cases the striped substance is separated from the blunt nerve-endings by some of the sarcoglia, which in some cases penetrate and traverse the other constituent of the fibre. The latter Kühne has called "rhabdia." The antler-like division of the axis-cylinder or spray, in contact with the muscular substance, serves to conduct the excitation from the former to the latter, but excitation of the muscular substance is never transmitted in the reverse order to the nerve-ending (*Kühne*).]

Fig. 376.

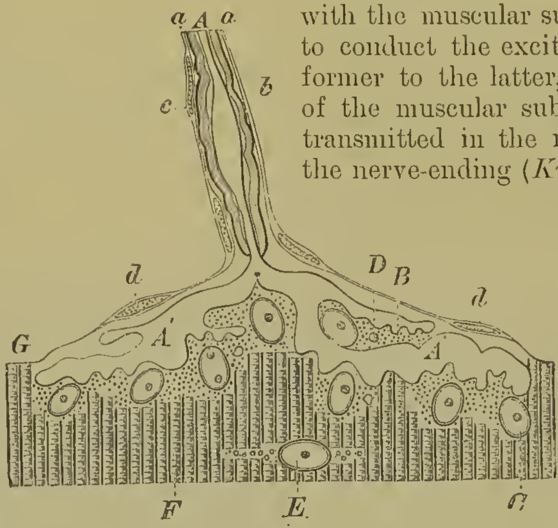


Fig. 377.

Fig. 376.—Motor nerve-ending in the frog (*Kühne*). *a*, Profile view of entrance of the nerve ; *b*, *b*, nuclei of the branches of the axial cylinder ; *c*, *c*, *c*, nuclei of Henle's sheath ; *e*, muscle nuclei. Fig. 377.—Motor nerve-ending in lizards, mammals, and man. Schematic after Kühne. A, axis-cylinder ; A^1, A^1, terminal branches of A ; *a*, *a*, myelin of nerves; *b*, perineural or Henle's sheath, and its nuclei (*c*); *d*, nuclei of telolemma ; B, bed ; D, large granule in B ; C, nuclei of the bed ; E, muscle nuclei ; F, contractile substance.

Each muscular fibre of the crayfish is supplied by two nerve-fibrils arising from separate axis-cylinders (*Biedermann*).

[Ramon y Cayal was unable to find any true eminences of Doyère in the wing-muscles of insects. By Golgi's method Cayal finds that there is revealed on the muscular fibres of Calliphora vomitoria a plexus of nerve-fibrils with nerve-cells at the nodes.]

Sensory fibres also occur in muscles, and they are the channels for muscular sensibility. They seem to be distributed on the outer surface of the sarcolemma where they form a branched plexus and wind round the muscular fibres (*Arndt*, *Sachs*); but, according to Tschirjew, the sensory nerves traverse the substance of the muscle, and after dividing dichotomously, end *only* in the aponeurosis, either suddenly or by means of a small swelling—a view confirmed by Rauber. The existence of sensory nerves in muscles is also proved by the fact that stimulation of the central end of a motor nerve, *e.g.*, the phrenic, causes increase of the blood-pressure and dilatation of the pupil (*Asp*, *Kowalewsky*, *Nawrocki*), as well as by the fact that when they are inflamed they are painful. They of course do not degenerate after section of the anterior root of the spinal nerves.

Red and Pale Muscles.—In many fishes (skate, plaice, herring, mackerel) (*W. Stirling*), birds, and mammals (rabbits), there are two kinds of striped muscle (*Krause*), differing in colour, histological structure (*Ranvier*), and physiological properties (*Kronecker and Stirling*). Some are "red," *e.g.*, the soleus and semitendinosus of the rabbit, and others "pale," *e.g.*, the adductor magnus. [All the muscles of the bat are red.] In the **pale muscles** the fibres are thinner, the transverse striation is thicker, their longitudinal striation less marked, and their nuclei fewer than in the red muscles (*Ranvier*) ; they contain less glycogen, water, and myosin. [W. Stirling finds that the red muscles in many fishes, *e.g.*, the mackerel, contain granules of oil, and present all the appearance of muscle in a state of fatty degeneration, while the pale muscles, lying side by side, contain no fatty granules.]

Julius Arnold found in human muscles an extensive distribution of pale fibres amongst

the red ones, and indeed in the same muscle in the frog and mammals, red and pale fibres occur together; in fact, this is the case in almost every muscle (*Grützner*).

[**Spectrum of Muscle.**—The red colour of the ordinary skeletal muscle is due to hæmoglobin in the sarcous substance (*Kühne*). This is proved by the fact that the colour is retained after all the blood is washed out of the vessels, when a thin muscle still shows the absorption-bands of hæmoglobin when examined with the spectroscope.]

[**Myo-hæmatin.**—MacMunn points out that although most voluntary muscles owe their colour to hæmoglobin, it is accompanied by *myo-hæmatin* in most cases, and sometimes entirely replaced by it (§ 293). Myo-hæmatin is found in the *heart* of vertebrates, in the papillary muscles of the human heart, and in abundance in the pectoral muscles of pigeons, and in some muscles of vertebrates and invertebrates, *e.g.*, certain beetles (Hydrophilus, Dytiscus), the common fly, and other insects, spiders, crustaceans, and molluscs.]

Muscular Fibres of the Heart.—The mammalian **cardiac muscle** has certain peculiarities already mentioned (§ 43):—(1) It is striped, but it is involuntary; (2) it has no sarcolemma; (3) its fibres branch and anastomose; (4) the transverse striation is not so distinct, and it is sometimes striated longitudinally; (5) the nucleus is placed in the centre of each cell (see § 43). [The cardiac muscle, viewed from a *physiological* point of view, stands midway between striped and unstriped muscle. Its contraction occurs slowly and lasts for a long time (p. 99), while, although it is transversely striped, it is involuntary.]

[**Purkinje's Fibres.**—These fibres, which form a plexus of greyish fibres under the endocardium of the heart of ruminants, have been described already (fig. 38); the cells have, as it were, advanced only to a certain stage of development (§ 46).]

Development of Muscular Fibre.—Each muscular fibre is developed from a uni-nucleated cell of the mesoblast, which elongates into the form of a spindle. As the cell elongates, the nuclei multiply. The superficial or parietal part of the cell-substance shows transverse markings (fig. 366, 7), while the nuclei with a small amount of protoplasm are continuous along the axis of the fibre, where they remain in some animals, but in man they pass to the surface where they come to lie under the sarcolemma. The muscles of the young are smaller and have fewer fibres than those of adults (*Budge*). In developing muscle, the number of fibres is increased by the proliferation of the muscle-corpuscles, which form new fibres.

According to Paneth, in old individuals separate cells with aggregation of contractile substance—so-called **Sarcoplasts**—unite to form new muscular fibres. Sig. Mayer regards these structures as retrogressive structures, and he calls them **Sarcolytes** (§ 103, II.).

Occurrence in lower Animals.—Striped muscle, besides occurring in the corresponding organs of vertebrata, occurs in the iris and choroid of birds. The arthropoda have only striped muscle, the molluscs, worms, and echinoderms chiefly smooth muscles; in the latter are muscles with double oblique striation (*Schwalbe*).

2. **Non-striped Muscle.**—[**Distribution.**—It occurs very widely distributed in the body, in the muscular coat of the lower half of the human œsophagus, stomach, small and large intestine, muscularis mucosæ of the intestinal tract, in the arteries, veins, and lymphatics, posterior part of the trachea, bronchi, infundibula of the lung, muscular coat of the ureter, bladder, urethra, vas deferens, vesiculæ seminales, and prostate; corpora cavernosa and spongiosa penis, ovary, Fallopian tube, uterus, skin, ciliary muscle, iris, upper eyelid, spleen and capsule of lymphatic glands, tunica dartos of the scrotum, gall-bladder, in ducts of glands, and in some other situations.]

[**Structure.**—Smooth muscular fibres consist of fusiform or spindle-shaped elongated cells, with their ends either tapering to fine points or divided (fig. 378). These contractile fibre-cells may be isolated by steeping a piece of the tissue in a 30 per cent. solution of caustic potash, or a strong solution of nitric acid. They are 45 to 230 μ [$\frac{1}{600}$ to $\frac{1}{120}$ in.] in length, and 4 to 10 μ [$\frac{1}{6000}$ to $\frac{1}{2500}$ in.] in breadth, Each cell contains a solid oval elongated **nucleus**, which may contain one or more nucleoli. It is brought into view by the action of dilute acetic acid, or by staining reagents. The mass of the cell appears more or less homogeneous, although in some places the cell-substance shows longitudinal fibrillation, [and is surrounded by a thin elastic envelope. They are not doubly refractive, so that the anisotropous substance seems to be absent]. [**Method.**—This fibrillation is revealed

more distinctly thus:—Place the mesentery of a newt (*Klein*) or the bladder of the salamandra maculata (*Flemming*) in a 5 per cent. solution of ammonium chromate, and afterwards stain it with picro-carmine. Each cell consists of a thin **elastic sheath** (sarcolemma of Krause) enclosing a bundle of **fibrils** (F) which run in a longitudinal direction within the fibre (fig. 379). They are continuous at the poles of the nucleus with the plexus of fibrils which lies within the nucleus, and, according to Klein, they are the contractile part, and when they contract the sheath becomes shrivelled transversely and exhibits what looks like thickenings (S). These fibrils have been observed by Flemming in the cells while *living*. Sometimes the cells are branched, while in the frog's bladder they are triradiate.]

[**Arrangement of the fibres.**—Sometimes the fibres occur singly, but usually they are arranged in groups, forming lamellæ, sheets, or bundles, or in a plexiform

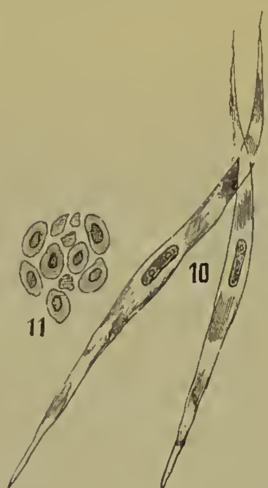


Fig. 378.

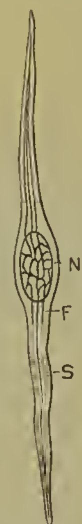


Fig. 379.

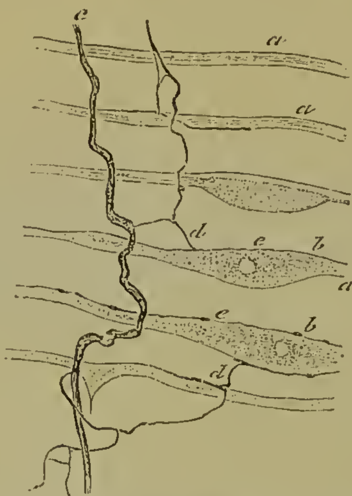


Fig. 380.

Fig. 378.—Smooth muscular fibres (10); (11) transverse section. Fig. 379.—Smooth muscular fibre from the mesentery of a newt (ammonium chromate). N, nucleus; F, fibrils; S, markings in the sheath. Fig. 380.—Termination of nerve in non-striped muscle.

manner, the bundles being surrounded by connective-tissue.] A very delicate elastic cement-substance unites the individual cells to each other. [This **cement** may be demonstrated by the action of nitrate of silver. In transverse section (fig. 378, 11) they appear oval or polygonal, with the delicate homogeneous cement between them; but, as the fibres are cut at various levels, the areas are unequal in size, and all of them, of course, are not divided at the position of the nucleus.]

They vary in length from $\frac{1}{100}$ to $\frac{1}{200}$ of an inch; those in the middle coat of the arteries are short, while they are long in the intestinal tract, and especially so in the pregnant uterus. According to Engelmann, the separation of the smooth muscular substance into its individual spindle-like elements is a *post-mortem* change of the tissue. [Sometimes transverse thickenings are seen, which are not due to transverse striation, but to a partial contraction. Occasionally they have a tendinous insertion.]

Blood-vessels in Smooth Muscle.—Non-striped muscle is richly supplied with blood-vessels, and the capillaries form elongated meshes between the fibres, [although it is not so vascular as striped muscle.] **Lymphatics** also occur between the fibres.

Motor Nerves to Smooth Muscle.—According to J. Arnold, they consist of medullated and non-medullated fibres [derived from the sympathetic system] which form a plexus—**ground plexus**—partly provided with ganglionic cells, and lying in

the connective-tissue of the perimysium. [The fibres are surrounded with an endothelial sheath.] Small branches [composed of bundles of fibrils] are given off from this plexus, forming the **intermediary plexus** with angular nuclei at the nodal points. It lies either immediately upon the musculature or in the connective-tissue between the individual bundles. From the intermediary plexus, the finest fibrillæ (0·3 to 0·5 μ) pass off, either singly or in groups, and reunite to form the **intermuscular plexus** (fig. 380, *d*), which lies in the cement substance between the muscle-cells, to end, according to Fränkenhauser, in the nucleoli of the nucleus, or in the neighbourhood of the nucleus (*Lustig*). According to J. Arnold, the fibrils traverse the fibre and the nucleus, so that the fibres appear to be strung upon a fibril passing through their nuclei. According to Lowit, the fibrils reach only the interstitial substance, while Gscheidlen also observed that the finest terminal fibrils, one of which goes to each muscular fibre, ran along the margins of the latter (fig. 380). The course of these fibrils can only be traced after the action of gold chloride. [Ranvier has traced their terminations in the stomach of the leech.]

[**Muscle-spindles.**—Here and there in muscles there exist peculiar bundles of muscular fibres or single fibres, to which there proceeds a large nerve-fibre enveloped in several sheaths. The nerve perforates the sheath and terminates in the muscular fibre or fibres. They were first described by Kölliker in 1862, and the above name was given them by Kühne in 1863. They appear to exist in all classes of vertebrates. These bodies were afterwards called **sarcoplasts** by Kühne. Similar bodies were described by Roth as "neuro-muscular trunklets." In frogs' muscles they consist of groups of 3–10 very fine muscular fibres supplied by a large nerve-fibre covered with several sheaths, and as they are thickest where the nerve enters, and taper somewhat towards their extremities, they received from Kühne, the name of "muscle-spindles," although Kölliker called them "muscle-buds." As Ranvier points out, the sheaths are not unlike the lamellated sheath of a nerve. These structures occur in the muscles of frogs, reptiles, and higher animals, and even in human muscles; they seem to be muscular fibres in process of dividing longitudinally (*Kölliker*), although Bremer regards them as muscular fibres in process of development.]

[**Structure of Tendon.**—A tendon consists chiefly of white fibrous tissue, with a very few elastic fibres. The white fibres are, for the most part, arranged longitudinally, and if a tendon be macerated in picric acid or 10 per cent. solution of common salt and then frayed out at one end, the fine delicate fibrils which compose the fibres are readily obtained. The fibres are partially covered by the tendon-cells, which are simply modified connective-tissue corpuscles. In a longitudinal section of a tendon the cells appear as fusiform nucleated cells lying in rows, in single file, between the bundles. If, however, the tendons, *e.g.*, from the tail of a rat or mouse, are stained with gold choride, the gold stains the protoplasm of the tendons deeper than the fibres, so that then the shape and relation of the cells can be more readily studied. The cells are flattened quadrilateral plates, which clasp the fibrous bundles, covering them, however, only on one side. They lie in rows on the fibres (fig. 381).

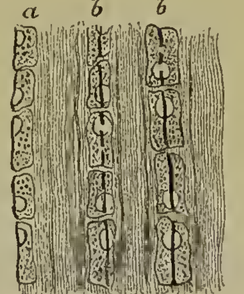


Fig. 381.

Tendon-cells, tail of a rat. *a*, Cells, tendon seen on edge and embracing a fibre; *b b*, on the flat, and showing their nuclei and ridges.

The nuclei of the cells are generally less deeply stained and usually lie at the contiguous borders of two adjacent cells, as if the two cells had been produced by the splitting of one cell. Each cell has on it a longitudinal "stripe" or "ridge" (fig. 381, *b*) much like the ridge seen on the tiles of a roof. The ridge is produced by the soft plastic cell being compressed between several adjacent fibres. The fibres are arranged in groups, forming longitudinal bundles, and these again are held together by a common **fibrous sheath**, which sends in septa between the bundles to support them, and bind them together. Thus, in a transverse section

of a tendon, one sees that the white fibres of the sheath and septa run somewhat circularly, and that they carry the few nerves and blood-vessels present in tendon. In the cross-section of each bundle are to be seen a number of stellate or branched spaces (fig. 382), lying between the smaller bundles of fascicules that make up a layer of bundles. These are the interfascicular or cell-spaces. In them lie the tendon-cells, of course closely applied to their respective fibres, and also some lymph. Each tendon externally is covered with an endothelial sheath.]

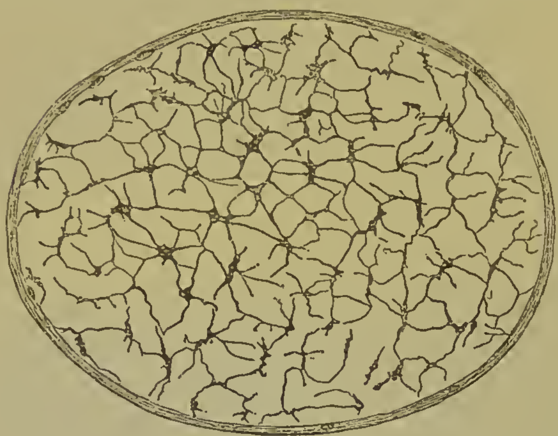


Fig. 382.
Transverse section of a tendon from the tail of a rat, showing the branched stellate spaces.

[**Physical properties of tendon.**—Moist tendon is highly flexible, is very inelastic and inextensible. It requires a very considerable force to rupture a tendon. The tendon of the frog's gastrocnemius will readily carry a weight of two to three pounds without being ruptured.]

[**Termination of Nerves in Tendon.**—For a long time it was believed that there were no nerves in tendon, but the fact that sprains are so painful, and that inflammation of tendons gives rise to severe pain, shows that there are sensory nerves present. The existence of nerve-terminations has been demonstrated in the tendons of all classes of vertebrates. They are readily obtained by the gold method in the sterno-radial tendon of the frog, and, as shown by Golgi, they are most abundant near the muscle. Medullated nerve-fibres can be traced to the tendon, where the axis-cylinder splits up into a number of fibrils, which unite amongst themselves, and form a **reticulated end-plate** (Golgi's end-plate), which is sometimes embedded in a

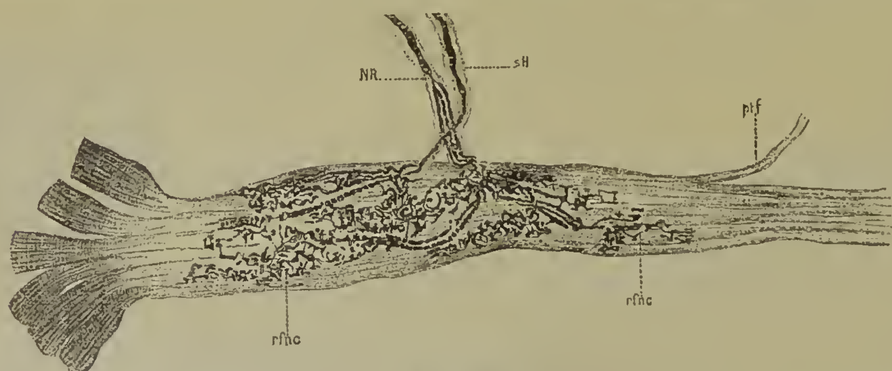


Fig. 383.
Termination of a nerve in the human tendo Achillis. NR, node of Ranvier; SH, sheath of Henle; *rfnc*, final ramifications of the axis-cylinder in bands; *ptf*, primitive bundles of the tendon.

granular-looking matter. The chief researches were made by Sachs (1875), Rollett (1876), and Golgi (1880), and most recently by Ciaccio. Golgi called the small tendon and the termination of the nerves in them "musculo-tendinous organs," but this name is not well chosen. The nerve-fibres which proceed to the tendon are always medullated; they lose their sheaths, and penetrate between the bundles of fibres of the tendon, where the axis-cylinder ramifies, and terminates either in free ends, or sometimes as a spiral round the tendon fibres. The

nerve-end plaques of tendon have no nuclei belonging to them like those of motor nerve-plates; they are simply a bushy termination of branches of the axis-cylinder (fig. 383), and are usually arranged in two or three planes in a tendon, and never on the exterior of the tendon. In some situations, especially in fasciæ, structures somewhat resembling end-bulbs have been found.]

Within the tendons of the frog there is a plexus of medullated nerve-fibres, from which brush-like divided fibres proceed, which ultimately end with a point in nucleated plates, the **nerve-flakes** of Rollett. According to Sachs, bodies like **end-bulbs** occur in tendons, while Rauber found **Vater's corpuscles** in their sheaths; Golgi found, in addition, **spindle-shaped terminal corpuscles**, which he regards as a specific apparatus for estimating tension.

293. **PHYSICAL AND CHEMICAL PROPERTIES OF MUSCLE.**—1. The **consistence** of the sarcous substance is the same as that of living protoplasm, *e.g.*, of lymph-cells; it is semi-solid, *i.e.*, it is not fluid to such a degree as to flow like a fluid, nor is it so solid that, when its parts are separated, these parts are unable to come together to form a continuous whole. The consistence may be compared to a jelly at the moment when it is dissolved (*e.g.*, by heat).

Proofs.—The following facts corroborate the view expressed above:—(*a*) The analogy between the function of the sarcous substance and the contractile protoplasm of cells (§ 9). (*b*) The so-called **Porret's phenomenon**, which consists in this, that when a galvanic current is conducted through the living, fresh, sarcous substance, the contents of the muscular fibre exhibit a streaming movement from the positive to the negative pole (as in all other fluids), so that the fibre swells at the negative pole (*Kühne*). (*c*) By the fact that wave-movements have been observed to pass along the muscular fibre. (*d*) Direct observation has shown that a small parasitic round worm (Myoryctes Weismanni) moved freely in the sarcous substance within the sarcolemma, while the semi-solid mass closed up in the tract behind it (*Kühne*, *Eberth*).

2. **Polarised Light.**—The contractile substance doubly refracts light, and is said to be **anisotropous**, while the ground-substance causes single refraction, and is **isotropous**. According to Brücke, muscle behaves like a doubly refractive, positive uniaxial body, whose optical axis lies in the long axis of the fibre. When a muscular fibre is examined under the polarisation microscope, the doubly refractive substance is recognised by its appearing *bright* in the dark field of the microscope when the Nicols are crossed (§ 297); in a coloured field (purple, red, *e.g.*, by inserting a plate of mica) these parts assume a different colour (blue, yellowish-red, or yellow). During **contraction of a muscular fibre**, the contractile part of the fibre becomes narrower, and at the same time broader, whilst the optical constants do not thereby undergo any change. Hence Brücke concludes that the contractile discs are not simple bodies like crystals, but must consist of a whole series of small doubly refractive elements arranged in groups, which change their position during contraction and relaxation. These small elements Brücke called **disdiaclasts**. According to Schipiloff, Danielewsky, and O. Nasse, the contractile anisotropous substance consists of myosin, which occurs in a crystalline condition, and represents the disdiaclasts. According to Engelmann, however, all contractile elements are doubly refractive, and the direction of contraction always coincides with the optical axis.

As regards the **anisotropous substance**, the investigation of v. Ebner have shown that during the process of growth of the tissue, *tension* is produced—the tension of bodies subjected to imbibition—which results in double refraction, and so gives rise to the condition called anisotropous. During a sustained contraction in a dying muscle, the index of refraction of the muscular fibre increases, which is due to the loss of water by the tissue, thus causing a greater concentration of the dissolved muscular constituents (*Exner*).

[**Reaction of Muscle.**—If a transverse section of a living excised muscle be pressed upon a strip of blue litmus paper, the latter may assume a reddish tinge, and if upon a red litmus paper the latter may assume a bluish tinge, but it will not alter violet litmus paper. This is the amphochromatic or amphoteric reaction, indicating that the muscle is neutral. It may, however, give only an alkaline reaction. A living muscle plunged into boiling water still retains its neutral or alkaline reaction; but a muscle, which has been tetanised, or is in rigor mortis, is decidedly acid.]

[**Chemical Composition of Muscle.**—Living muscle in the resting condition is alkaline in reaction and has in round numbers the following composition:—

Water, 75 per cent.	Proteids and albuminoids, 21 per cent.
Solids, 25 ,, ,,	Fats, extractives, and salts, 4 ,, ,,

The human pectoralis major gave :—

Water, ...	73·5
Solids, ...	26·5
Proteids, including sarcolemma, and proteids of connective-tissue and vessels, ...	18·02
Gelatin } from connective-tissue, ...	1·99
Fat } from connective-tissue, ...	3·27
Extractives (kreatin, lactic acid, &c.), ...	0·22
Inorganic salts, ...	3·12]

The **chemical composition** of muscle rapidly undergoes a great change after death, owing to the spontaneous coagulation of a proteid within the muscular fibres. As frog's muscles may be frozen and thawed, and still remain contractile, they cannot therefore be greatly changed by the process of freezing. Kühne bled frogs, cooled their muscles to 10° or 7° C., pounding them in an iced mortar, and expressed their juice through linen. The juice so expressed, when filtered in the cold, forms a neutral, or alkaline, slightly yellowish, opalescent fluid, the so-called "**muscle-plasma.**" Like blood-plasma, it coagulates spontaneously; at first it is like a uniform soft jelly, but soon becomes opaque; doubly refractive fibres and specks, similar to the fibrin of blood, appear in the jelly, and as these begin to contract, they squeeze out of the jelly an *acid* "**muscle-serum.**" [Halliburton finds that the muscles of warm-blooded animals yield a similar muscle-plasma when they are cooled and subjected to pressure in a suitable press.] Cold prevents or delays the coagulation of the muscle-plasma; above 0° coagulation occurs very slowly, and the rapidity of coagulation increases rapidly as the temperature rises, while coagulation takes place very rapidly at 40° C. in cold-blooded animals, or at 48° to 50° C. in warm-blooded muscles. The addition of distilled water or an acid to muscle-plasma causes coagulation at once. The coagulated proteid most abundant in muscle, and which arises from the doubly refractive substance, is called "**myosin**" (*W. Kühne*).

Myosin.—It is a globulin (§ 245), and is soluble in strong (10 per cent.) solution of common salt, and is again precipitated from such a solution by dilution with water, or by the addition of very small quantities of acids (0·1 to 0·2 per cent. lactic or hydrochloric acid). It is soluble in dilute alkalies or slightly stronger acids (0·5 per cent. lactic or hydrochloric acid), and also in 13 per cent. ammonium chloride solution. [The more myosin is freed from salts (especially of calcium) by washing, the more insoluble does it become, both in saline solutions and weak hydrochloric acid. When once precipitated from its solution, it can be redissolved, reprecipitated, and again undergo coagulation a second or even a third time (*Halliburton*).] Like fibrin, myosin rapidly decomposes hydric peroxide. When treated with dilute hydrochloric acid and heat, it is very rapidly changed into syntonin (§ 245). Myosin may be extracted from muscle by a 10 to 15 per cent. solution of NH_4Cl, and if it be heated to 65°, it is precipitated again (*Danielewsky*). Danielewsky succeeded in partly changing syntonin into myosin by the action of milk of lime and ammonium chloride. Myosin occurs in other animal structures (cornea), nay, even in some vegetables (*O. Nasse*).

Muscle-serum, according to Kühne, still contains three proteids (2·3 to 3 per cent.), viz. :—1. **Alkali-albuminate**, which is precipitated on adding an acid, even at 20° to 24° C. 2. Ordinary **serum-albumin**, 1·4 to 1·7 per cent. (§ 32, *a*), which coagulates at 73° C. 3. An albuminate which coagulates at 47° C.

[Halliburton finds, however, the following **proteids in muscle-plasma.**—

Name.	Precipitated by Heat at	Saturation with NaCl or Na_2SO_4.	
Paramyosinogen, ...	47° C.	Causes precipitation.	Proteids which go to form muscle-clot.
Myosinogen, ...	56°	,, ,,	
Myoglobulin, . . .	63°	,, ,,	Proteids of the muscle serum.
Albumin, ...	73°	No ↓	
Myoalbumose, ...	Not ↓	No ↓	

Although the first two go to form the clot of muscle or myosin, paramyosinogen is not essential for coagulation. Besides these bodies there are **hæmoglobin** and also **myo-hæmatin**, which is not identical with the blood-pigment (? p. 472). The latter can be extracted by ether from muscle (*e.g.*, the breast muscle of a pigeon), whereby the ether becomes red. It can exist in an oxidised and reduced condition (*MacMunn*). According to Levy, it is identical with hæmochromogen, while Hoppe-Seyler regards it as a mixture of HbO_2 and Hb.]

The other chemical constituents of muscle have been referred to in treating of flesh (§ 233). 1. **Muscle-ferments.**—Brücke found traces of **pepsin** and peptone in muscle-juice, [the latter is denied by Halliburton]; Piotrowsky, a trace of a **diastatic ferment.** [When muscle becomes acid, as in rigor mortis, the pepsin at a suitable temperature (35° to 40° C.) acts on the proteids, and albumoses and peptones are formed. Halliburton found a **myosin-ferment** which has the characters of an albumose. It is prepared in the same way as fibrin-ferment by keeping muscle for some months under alcohol, and then making a watery extract of the muscle. It does not hasten the coagulation of blood-plasma, although it causes muscle-plasma to coagulate. It does not seem to be identical with fibrin-ferment.] 2. In addition to volatile *fatty acids* (formic, acetic, butyric), there are two isomeric forms of **lactic acid** ($C_3H_6O_3$) present in muscle with an acid reaction :—(*a*) *Ethylidene-lactic acid*, in the modification known as right rotatory *sarcolactic* or *paralactic* acid, which occurs only in muscles, and some other animal structures. (*b*) *Ethylene-lactic acid* in small amount (§ 251, 3, *c*). It was formerly assumed that lactic acid is formed by fermentation from the carbohydrates of the muscle (glycogen, dextrin, sugar), and Maly has observed that paralactic acid is occasionally formed when these bodies undergo fermentation. According to Böhm, however, the glycogen of muscle does not pass into lactic acid, as during rigor mortis, if putrefaction be prevented, the amount of glycogen does not diminish. If muscle be suddenly boiled or treated with strong alcohol, the ferment is destroyed, and hence the acidification of the muscular tissue is prevented (*Du Bois-Reymond*). *Acid potassium phosphate* also contributes to the acid reaction. 3. **Glycogen** occurs to the amount of over 1 per cent. after copious flesh feeding, and to 0·5 per cent. during fasting. It is stored up in the muscles, as well as in the liver during digestion, but it disappears during hunger. It is perhaps formed in the muscles from proteids (§ 174, 2). 4. *Carnin* ($C_7H_8N_4O_3$) which is changed by bromine or nitric acid into sarkin, occurs to the extent of 1 per cent. in Liebig's extract of meat (*Weidel*). 5. *Urea*, 0·01 per cent. (*Haycraft*). [There is much urea in the muscles of the skate and allied genera of fish.] 6. *Lecithin*, derived in part from the motor nerve-endings (§ 23 and § 251). 7. The **gases** are CO_2 (15 to 18 vol. per cent.), partly absorbed, partly chemically united (some absorbed N, but **no free O**, although muscle continually absorbs O from the blood passing through it (*L. Hermann*). The muscles contain a substance whose decomposition yields CO_2. When muscles are exercised, this substance is used up so that severely fatigued muscles yield less CO_2 (*Stinzing*). [All muscles have not the same chemical composition (p. 432).]

[The **extractives** of muscle are divided into—

(**A**) **Nitrogenous,** *e.g.*, Kreatin, $C_4H_9N_3O_2$ = 0·2 to 0·3 per cent. (This therefore indicates that a very considerable quantity of this substance (90 grams) must exist in the body, seeing that the muscles make up nearly one half of the weight of the body) : Kreatinin, $C_4H_7N_3O$; Hypoxanthin, $C_5H_4N_4O$; Xanthin, $C_5H_4N_4O_2$; Uric acid, $C_5H_4N_4O_3$; Carnin, $C_7H_8N_4O_3 + H_2O$; Urea, CON_2H_4 ; Taurin ; Inosinic acid, $C_{10}H_{14}N_4O_{11}$; Lecithin (?) which may be derived from the nerve-fibres in muscle.

(**B**) **Non-nitrogenous** ; glycogen, inosite, fermentable sugar, lactic acids, and fats.]

[**Chemistry of Smooth Muscle.**—Smooth muscle, as a rule, has an alkaline or neutral reaction, although the adductor muscle of Anodonta, which is almost constantly in action, is acid. Smooth muscles pass into rigor and become acid. A spontaneously coagulable plasma has so far not been obtained, nor has myosin. A body related to myosinogen coagulating at 45–49 C. has been obtained by Heidenhain. Smooth muscles are said to contain alkali-albuminate and an albumin coagulating at 75°C. (*Hammarsten*).]

294. METABOLISM IN MUSCLE.—[In living muscle we have to study the transformations of energy, and the chemical changes on which these depend. But as we cannot examine the chemical changes which occur during a contraction, we are confined to a study of—

(1) The composition of a muscle before and after contraction, and
(2) The effect of contraction on the medium surrounding or passing through a muscle.

We may observe the effect produced by a muscle upon air or other gases to which an excised muscle is exposed, or we may investigate the changes which the blood undergoes in passing through a muscle, and if the muscle be still *in situ*, the effect upon the general excreta. These methods may be applied to muscle in various conditions, passive or active, dead or dying, to excised muscles or those still under normal conditions.]

I. A passive muscle continually absorbs a certain amount of O from the blood flowing through its capillaries and returns a certain amount of CO_2 to the blood-stream. The amount of CO_2 given off is less than corresponds to the amount of O absorbed. Excised muscles freed from blood exhibit an analogous but diminished gaseous exchange. As an excised muscle remains longer excitable in O or in air than in an atmosphere free from O, or in indifferent gases, we must conclude that the above-named gaseous exchange is connected with the normal metabolism, and is a condition on which the life and activity of the muscle depend. Resting living muscles also exhale CO_2.

Perfusion of blood.—If a living muscle be excised (dog), and if blood be perfused through its blood-vessels, the amount of O used up is, within pretty wide limits, almost independent of temperature; if the variations of temperature be great, it rises and falls with the temperature. The CO_2 given off by muscular tissue (less than the O used up) falls when the muscle is cooled, but it is not increased when the muscle is subsequently warmed (*Rubner*).

Putrefaction.—This exchange of gases must be distinguished from the putrefactive phenomena due to the development of living organisms in the muscle. These putrefactive phenomena are also connected with the consumption of O and the excretion of CO_2 and occur soon after death (*L. Hermann*).

II. In an active muscle the **blood-vessels** are always **dilated** (*Ludwig and Sczelkow, Gaskell*)—a condition pointing to a more lively material exchange in the organ. The dilatation of the blood-vessels can be observed microscopically in the contracting mylo-hyoid muscle of the frog. If the motor-nerve passing to the mylo-hyoid muscle be stimulated, either with or without the use of curare, the blood-vessels dilate. This is due to the action of the vaso-dilator nerve-fibres on the smooth muscles of the blood-vessels, causing them to relax. Hence the active muscle is distinguished from the passive one by a series of chemical transformations.

1. **Reaction of Muscle.**—The neutral or feebly alkaline reaction of a passive muscle (also of the non-striped variety) passes into an *acid* reaction during the activity of the muscle, owing to the formation of paralactic acid (*Du Bois-Reymond*, 1859); the degree of acidity increases up to a certain extent, according to the amount of work performed by the muscle (*R. Heidenhain*). The acidification is due, according to Weyl and Zeitler, to the phosphoric acid produced by the decomposition of lecithin and (? nuclein).

It is doubtful if the acidity is due to lactic acid, as Warren and Astaschewsky find that there is less lactic acid in the active than in the passive muscle. Marcuse, however, supports the lactic acid theory, while Moleschott and Battistini agree that the passive muscle contains acid, but the fatigued muscle contains more, especially of phosphoric acid and CO_2.

2. **Production of CO_2.**—An active muscle excretes considerably more CO_2 than a passive one :—(*a*) active muscular exertion on the part of a man or of animals increases the amount of CO_2 given off by the lungs (§ 126, 6) ; (*b*) venous blood flowing from a tetanised muscle of a limb contains more CO_2, more CO_2 being formed than corresponds to the O which has simultaneously been absorbed (*Ludwig and Sczelkow*). The same result is obtained when blood is perfused through an excised muscle ; (*c*) an excised muscle caused to contract excretes more CO_2 (compare § 368).

3. **Consumption of Oxygen.**—An active muscle uses up more O—(*a*) when more muscular work is done, the body absorbs much more O (§ 217)—even 4 to 5 times as much (*Regnault and Reiset*) ; (*b*) venous blood flowing from an active muscle of a limb contains less O (*Ludwig, Sczelkow, and Al. Schmidt*). Nevertheless, the increase of O used up by the active muscle is not so great as the amount of CO_2 given off (*v. Pettenkofer and v. Voit*). The increase of O used up may be ascertained even during the period of rest directly following the period of activity, and the same is the case with the CO_2 excreted (*v. Frey*).

As yet it is not possible to prove by gasometric methods that O is used up in an **excised muscle** free from blood. Indeed, the presence of O does not seem to be absolutely necessary for the activity of muscle during short periods, as an excised muscle may continue to contract in a vacuum, or in a mixture of gases free from O, and no O can be obtained from muscular tissue (*L. Hermann*). A frog's muscles rob easily-reducible substances of their O ; they discharge the colour of a solution of indigo ; muscles which have rested for a time, acting less energetically than those which have been kept in a state of continued activity (*Grützner, Gscheidlen*).

[The following table quoted by Halliburton shows the consumption of oxygen and the elimination of CO_2 by living and rigid muscles, and that although the O absorbed is nearly identical in amount, the CO_2 given off is greatly increased by the onset of rigor and by contraction—

	Oxygen absorbed	CO_2 given off
Living muscle,	18 per cent.	8 per cent.
Rigid muscle,	16 ,,	16 ,,
Muscle at rest,	6 ,,	1 ,,
Tetanised muscle,	8 ,,	9 ,,

The same result is shown by an analysis of the blood after being perfused through passive and active surviving muscles (*Ludwig and Schmidt*):—

Venous blood.	O less than arterial blood.	CO_2 more than arterial blood.
Muscle at rest,	9·0 per cent.	6·7 per cent.
Muscle in action,	12·26 ,,	10·8 ,,]

4. **Glycogen.**—The amount of glycogen (0·43 per cent. in the muscles of a frog or rabbit) and grape-sugar is diminished in an active muscle (*O. Nasse, Weiss*), but muscles devoid of glycogen do not lose their excitability and contractility. Hence glycogen is certainly not the direct source of the energy in an active muscle. Perhaps it is to be sought for in an as yet unknown decomposition-product of glycogen (*Luchsinger*). [There is more glycogen in the red than in the pale muscles of a rabbit.]

[The question as to whether the glycogen of muscle is carried from the liver by the blood-stream to the muscles, or whether it is formed in the muscles themselves, has been answered in various ways. Külz observed in frogs whose livers were removed, that the amount of glycogen in the muscles increased after subcutaneous injection of sugar. The muscles also retain their glycogen for a longer time than does the liver during starvation. These facts indicate that the

glycogen is formed in the muscles themselves. The normal circulation is one of the conditions for glycogenesis of muscle, for ligature of all the vessels of a muscle is followed by diminution of its glycogen.]

[The muscle-glycogen is not so rapidly used up during starvation as that of the liver (p. 320). It is undoubtedly diminished during muscular work. Although removal of the liver diminishes the muscle-glycogen, this does not prove that the muscle-glycogen is derived from the hepatic glycogen. Section of a motor nerve to a muscle results in an accumulation of the glycogen in the muscle.]

5. **Extractives.**—An active muscle contains less extractive substances soluble in water, but more extractives soluble in alcohol (*v. Helmholtz*, 1845); it also contains less of the substances which form CO_2 (*Ranke*); less fatty acids (*Sczelkow*); less kreatin and kreatinin (*v. Voit*).

6. During contraction, the amount of **water** in the muscular tissue increases, while that of the blood is correspondingly diminished (*J. Ranke*). The solid substances of the blood are increased, while they (albumin) are diminished in the lymph (*Fano*).

7. **Urea.**—The amount of urea excreted from the body is not materially increased during muscular exertion (*v. Voit, Fick, and Wislicenus*). According to Parkes, however, although the excretion of urea is not increased immediately, yet after 1 to 1½ day there is a slight increase. The amount of work done cannot be determined from the amount of albumin which is changed into urea.

[**Relation of Muscular Work to Urea.**—Ed. Smith, Parkes, and others have made numerous investigations on this subject. Fick and Wislicenus (1866) ascended the Faulhorn,—one of the Swiss Alps, 1956 metres high. The actual amount of energy expended in the form of muscular movement was obtained by multiplying the body-weight of each experimenter by the height which each climbed. This in the case of Fick was 66 kilos. × 1956 = 129,096 kilogrammetres, and that of Wislicenus was 76 × 1956 = 148,656 kilogrammetres. On calculating the amount of energy obtainable from the decomposition of all the albuminous material used up, this only gave 66,690 kilogrammetres for Fick and 68,376 for Wislicenus, *i.e.*, only about the half of the energy expended. It was plain, therefore, that the proteids were not the sole source of the energy expended, and also that the quantity of urea excreted was not in proportion to the work done. For seventeen hours before and for six hours after the ascent no proteid food was taken—the diet consisting of cakes made of fat, sugar, and starch. The urine was collected in three periods as follows :—

	Fick.		Wislicenus.	
1. Urea of 11 hours before the ascent, .	238·55 grs.		221·05 grs.	
2. ,, 8 ,, during ,,	109·44 ,,	189·77	103·46 ,,	183·35
3. ,, 6 ,, after ,,	80·33 ,,		79·89 ,,	

A hearty meal was taken after this period, and the urine of the next eleven hours after the period of rest contained 159·15 grains of urea (*Fick*), and 176·71 (*Wislicenus*). All the experiments go to show that the amount of urea excreted in the urine is far more dependent upon the nitrogen ingested, *i.e.*, the **nature of the food**, than upon the decomposition of the muscular substance. A vegetable diet diminishes, while an animal diet greatly increases, the amount of urea in the urine. North's researches confirm those of Parkes, but he finds that the disturbance produced by severe muscular labour is considerable. The elimination of phosphates is not affected, while the sulphates in the urine are increased.]

According to Argutinsky, who conducted his experiments under Pflüger's direction, increased muscular exertion (mountain climbing) causes a considerable increase in the elimination of N by the urine, which may last for three days. On calculating from the increased amount of N the amount of albumin that must have been decomposed in the body during the increased work-period, it was found that a very considerable amount of the work must have been due to the decomposition of proteids. J. Munk, however, challenges the correctness of these results on the ground that the experimenter was not in a satisfactory condition as regards nutrition.

During the **activity of a muscle**, *all* the groups of the chemical substances present in muscle undergo more rapid transformations (*J. Ranke*). It is still a matter of doubt, therefore, whether we may assume that the kinetic energy of a muscle is chiefly due to the transformation of the chemical energy of the carbohy-

drates which are decomposed or used up in the process of contraction. As yet we do not know whether the glycogen is supplied by the blood-stream to the muscles, perhaps from the liver, or whether it is formed within the muscles themselves from some unknown derivative of the proteids. The normal circulation is certainly one of the conditions for the formation of glycogen in muscle, as glycogen diminishes after ligature of the blood-vessels (*Chandelon*). A muscle in which the blood circulates freely is capable of doing more work than one devoid of blood, and even in the intact body, more blood is always supplied to the contracted muscles.

[**Sources of Muscular Energy.**—The experiment of Fick and Wislicenus definitely proved that the proteids are not the exclusive, or by any means the chief, source of muscular energy. As it is conclusively proved that during muscular work there is a great increase in the amount of O absorbed, and CO_2 given off, it is evident that the non-nitrogenous substances of the food must be the chief sources of this energy. We turn naturally to the carbohydrates, and as the latter are chiefly stored up in the form of glycogen in the muscles, it is assumed that glycogen is the chief source of the energy. Glycogen in muscle diminishes during muscular work, and is stored up during rest (*Bernard*). Külz also found that in dogs the glycogen disappears from the liver during work, and Voit found that the muscle-glycogen disappears before that in the liver. But frog's muscles still contract, and do work, although they may contain no glycogen. It appears, therefore, that the *carbohydrates* are a source of muscular energy. But they, again, are not the only source. It is highly probable that glycogen can be formed from proteids, and it is allowable, therefore, to assume that *proteids* may also serve as a source of muscular energy. If this be not so, it is difficult to understand how carnivora can be fed and maintained in good health for long periods on lean flesh. The fats are probably also another source. Hence it would appear that all three of the chief groups of food-stuffs—carbohydrates, proteids, and fats—*may* serve as the source of muscular energy; but that, so long as non-nitrogenous elements are supplied in the food in sufficient quantity, or are stored up in the body, the muscles do their work chiefly on these. After they are used up, the proteids are, as it were, called up.]

[The metabolism of muscle appears to be regulated by the central nervous system (*Pflüger*, *Zuntz*). Even when at rest in the ordinary sense, *i.e.*, when the muscles are not doing any mechanical work, the muscle is in a condition which Zuntz and Röhrig have called "chemical tonus." It appears to be a reflex tonus, so that it can be set aside by severing the connection between the muscle and the central nervous system, and this may be done either by section of the motor nerve, or by the action of curare.]

295. RIGOR MORTIS.—**Cause.**—Excised striped, or smooth muscles, and also the muscles of an intact body, at a certain time after death, pass into a condition of rigidity —**cadaveric rigidity** or **rigor mortis**. When all the muscles of a corpse are thus affected, the whole cadaver becomes completely stiff or rigid. The **cause** of this phenomenon depends upon the spontaneous coagulation of a proteid, viz., the **myosin** within the sarcolemmas of the muscular fibres (*Kühne*). Under certain circumstances the coagulation of the other proteids of the muscle may increase the rigidity. During the process of coagulation, an acid is formed, heat is set free (*v. Walther*, *Fick*—§ 223), owing to the passage of the fluid myosin into the solid condition, and also to the simultaneous and subsequently increased density of the tissue.

Properties of a Muscle in Rigor Mortis.—It is shorter, thicker, and somewhat denser (*Schmulewitsch*); stiff, compact, and solid; turbid and opaque (owing to the coagulation of the myosin); incompletely elastic, less extensible, and more easily torn or ruptured; it is completely inexcitable to stimuli; the muscular

electrical current is abolished, (or there is a slight current in the opposite direction), [a dead muscle is negatively electrical to a living one], its reaction is *acid*, owing to the formation of both forms of lactic acid (§ 293), and glycero-phosphoric acid (*Diakanow*); while it also develops free CO_2. When an incision is made into a rigid muscle, a fluid, the muscle-serum, appears spontaneously in the wound (§ 293).

The first formed lactic acid converts the salts of the muscle into acid salts; thus, potassium lactate and acid potassium phosphate are formed from potassium phosphate. The lactic acid, which is formed thereafter, remains free and ununited in the muscle.

Amount of Glycogen.—The newest observations of Böhm are against the view that, during rigor mortis, a partial or complete transformation of the glycogen into sugar and then into lactic acid takes place. During digestion, a temporary storage of glycogen occurs in the muscles as well as in the liver, so that about as much is found in the muscles as in the liver. There is no diminution of the glycogen when rigidity takes place, provided putrefaction be prevented; so that the lactic acid of rigid muscles cannot be formed from glycogen, but more probably it is formed from the decomposition of the albuminates (*Demant*, *Böhm*).

The **amount of acid** does not vary, whether the rigidity occurs rapidly or slowly (*J. Ranke*); when acidification begins, the rigidity becomes more marked, owing to the coagulation of the alkali-albuminate of the muscle. Less CO_2 is formed from a rigid muscle the more CO_2 it has given off previously, during muscular exertion. A rigid muscle gives off N, and absorbs O. In a cadaveric rigid muscle, **fibrin-ferment** is present (*Al. Schmidt and others*). It seems to be a product of protoplasm, and is never absent where this occurs (*Rauschenbach*). [The myosin-ferment seems not to be identical with the fibrin-ferment (p. 577).]

[**Rigor Mortis and Coagulation of Blood.**—Thus there is a marked analogy between the coagulation of the blood and that of muscle. In both cases, a fluid body yields a solid body, fibrin from blood, and myosin from muscle; the coagulation of blood is prevented by neutral salts, and so is the coagulation of myosin; dilution of the salted plasma produces coagulation in both cases; and perhaps the coagulation in both is due to the action of a ferment, the one the fibrin-ferment, the other the myosin-ferment. There are, however, points of difference, for myosin can be dissolved, reprecipitated, and coagulated several times, while fibrin does not undergo recoagulation; the formation of myosin from myosinogen, again, is accompanied by the development of an acid, whereas that of fibrin from fibrinogen is not; further, the formation of myosin is not accompanied by the formation of another globulin, whereas that of fibrin from fibrinogen is.]

Stages of Rigidity.—Two stages are recognisable in cadaveric muscles:—In the **first stage**, the muscle is rigid, but still excitable; in this stage the myosin seems to be in a jelly-like condition. Restitution is still possible during this stage. In the **second stage**, the rigidity is well pronounced, with all the phenomena above mentioned.

The **onset of the rigidity** varies in man from ten minutes to seven hours [but as a rule it is complete within four to six hours after death. The muscles of the jaws are first affected, then those of the neck and trunk, afterwards (as a rule) the lower limbs, and finally the upper limbs]. Its **duration** is equally variable—one to six days. After the cadaveric rigidity has disappeared, the muscles, owing to further decompositions and an alkaline reaction, become soft, and the rigidity disappears (*Nysten*). The onset of the rigidity is always preceded by a loss of nervous activity. Hence, the muscles of the head and neck are first affected, and the other muscles in a descending series (§ 352). Disappearance of the rigidity occurs first in the muscles first affected (*Nysten*). Great muscular activity before death (*e.g.*, spasms of tetanus, cholera, strychnin, or opium poisoning) causes rapid and intense rigidity; hence, the heart becomes rigid relatively rapidly, and strongly. Hunted animals may become affected within a few minutes after death. Usually the rigidity lasts longer the later it occurs. Rigidity does not occur in a fœtus before the seventh month of intra-uterine life. A frog's muscle cooled to 0° C. does not begin to exhibit cadaveric rigidity for four to seven days.

Stenson's Experiment.—The amount of blood in a muscle has a marked effect upon the onset of the rigidity. Ligature of the muscular arteries causes at first in all mammals an increase of the muscular excitability, and then a rapid fall of the excitability (*Schmulewitsch*); thereafter stiffness occurs, the one stage following closely upon the other (*Swammerdam*, *Nic. Stenson*, 1667). [If the ligature be removed in the first stage, the muscle recovers, but in the later stages the rigidity is permanent.] If the artery going to a muscle be ligatured, Stannius observed that the excitability of the motor nerves disappeared after an hour, that of the muscular substance after four to five hours, and then cadaveric rigidity set in.

Pathological.—When the blood-vessels of a muscle are occluded, by coagulation taking place within them, rigidity of the muscles is produced (§ 102). True cadaveric rigidity may be produced by too tight bandaging; the muscles are paralysed, rigid, and break up into flakes, while the contents of the fibre are afterwards absorbed (*R. Volkmann*). Occlusion of the blood-vessels of muscles by infarcts, especially in persons with atheromatous arteries, may even cause necrosis of the muscles implicated (*Finch*, *Girandeau*). In a completely anæmic limb, the sensory nerves are still excitable for 5–10 hours (*Stefani*).

If the circulation be re-established during the first stage of the rigidity, the muscle soon recovers its excitability (*Stannius*). When the second stage has set in, restitution is impossible (*Kühne*). In cold-blooded animals, cadaveric rigidity does not occur for several days after ligaturing the blood-vessels. Brown-Séquard, by injecting fresh oxygenated blood into the blood-vessels, succeeded in restoring the excitability of the muscles of a human cadaver four hours after death, *i.e.*, during the first stage of cadaveric rigidity. Ludwig and Al. Schmidt found that the onset of cadaveric rigidity was greatly retarded in excised muscles, when arterial blood was passed through their blood-vessels. Blood deprived of its O did not produce this effect. Cadaveric rigidity occurs relatively early after severe hæmorrhage. If a weak alkaline fluid be perfused through the blood-vessels of the dead muscles of a frog, cadaveric rigidity is prevented (*Schipiloff*).

Section of Nerves.—Preliminary **section of the motor nerves** causes a later onset of the rigidity in the corresponding muscles (*Brown-Séquard*, *Heineke*). [The same result occurs after a hemi-section of the spinal cord or after removal of one cerebral hemisphere (*Bierfreund*).] In fishes, whose medulla oblongata is suddenly destroyed, cadaveric rigidity occurs much more slowly than in those animals that die slowly (*Blane*).

[**Other Influences.**—Rigidity begins much later in the red (11 to 15 hours) than in pale muscles (1 to 3 hours post mortem); the rigor is complete in the white muscles in 10 to 14 hours, in the red in 52 to 58 hours. The extent of shortening due to the rigor is 2 to 2½ times as great as in the white. In both muscles the resolution of the rigor begins 12 to 15 hours after the completion of the rigidity, so that the red muscles are not completely rigid before the other muscles appear to have passed from a state of rigidity. Temperature has a marked effect, but it acts more on the resolution than on the onset of the rigor. At 60° C. the onset begins almost at once, and is complete in a few minutes (*Bierfreund*). Ether and chloroform injected into the blood-vessels cause almost instantaneous rigor (*Kussmaul*).]

Rigidity may be produced **artificially** by various reagents:—

1. **Heat** [**"Heat-stiffening"**] causes the myosin to coagulate at 40° C. in cold-blooded animals, in birds about 53° C., and in mammals at 48° to 50° C. The protoplasm of plants and animals, *e.g.*, of the amœba, is coagulated by heat, giving rise to heat-rigor.

Schmulewitsch found that the longer a muscle had been excised from the body, the greater was the heat required to produce stiffening. Heat-stiffening differs from cadaveric rigidity thus:—a 13 per cent. solution of ammonium chloride dissolves out the myosin from a cadaveric rigid muscle, but not from one rendered rigid by heat (*Schipiloff*). If the rigid cadaveric muscles of a frog be heated, another proteid coagulates at 45°, and lastly at 75° the serum-albumin itself. Hence, both processes together make the muscle more rigid (§ 295).

2. When a muscle is saturated with **distilled water** it produces **"water-stiffening"**—an acid reaction being developed at the same time.

Muscles rendered stiff by water still exhibit electromotive phenomena, while muscles rendered rigid by other means do not (*Biedermann*). If the upper limb of a frog be ligatured, deprived of its skin, and dipped in warm water, it becomes rigid. If the ligature be removed and the circulation re-established, the rigidity may be partially set aside. If there be well-marked rigidity, it can only be set aside by placing the limb in a 10 per cent. solution of common salt, which dissolves the coagulum of myosin (*Preyer*).

3. **Acids**, even CO_2 rapidly produce "**acid-stiffening**," which is probably different from ordinary stiffening, as such muscles do not evolve any free CO_2 (*L. Hermann*). The injection of 0·1 to 0·2 per cent. solutions of lactic or hydrochloric acid into the muscles of a frog produces stiffening at once, which may be set aside by injecting 0·5 per cent. solution of an acid, or by a solution of soda, or by 15 per cent. solution of ammonium chloride. The acids form a compound with myosin (*Schipiloff*). [The stiffening produced by acids and hot water is quite different from the spontaneous rigor occurring after death.]

4. **Freezing** and **thawing** a part alternately rapidly produce stiffening; and it is aided by **mechanical injuries**.

Poisons.—Rigor mortis is favoured by quinine, caffein, digitalin, [a concentrated solution of caffein or digitalin, applied to the muscle of a frog, produces rigor mortis], veratrin, hydrocyanic acid, ether, chloroform, the oils of mustard, fennel, and aniseed; direct contact of muscular tissue with potassium sulphocyanide (*Bernard*, *Setschenow*), ammonia, alcohol, and metallic salts.

Position of the Body.—The attitude of the body during cadaveric rigidity is generally that occupied at death; the position of the limbs is the result of the varying tensions of the different muscles. During the occurrence of rigor mortis, a limb, or more frequently the arm and fingers, may move (*Sommer*). Thus, if stiffening occurs rapidly and firmly in certain groups of muscles, this may produce movements, as is sometimes seen in cholera. If cadaveric rigidity occurs very rapidly, the body may occupy the same position which it did at the moment of death, as sometimes happens on the battle-field. In these cases it does not seem that a contracted condition of the muscle passes at once into rigor mortis; but between these two conditions, according to Brücke, there is always a very short relaxation.

Muscles which have been plunged into **boiling water** do not undergo rigor mortis, neither do they become acid (*Du Bois-Reymond*), nor evolve free CO_2 (*L. Hermann*).

Work done during Rigidity.—A muscle in the act of becoming stiff will lift a weight, but the height to which it is lifted is greater with small weights, less with heavier weights, than when a living muscle is stimulated with a maximal stimulus.

Analogy between Contraction and Rigidity.—L. Hermann has drawn attention to the analogy which exists between a muscle in a state of contraction and one in a state of cadaveric rigidity—both evolve CO_2 and the other acids from the same source; [both acts take place without the consumption of O]. The form of the contracted and of the stiffened muscles is shorter and thicker; both are denser, less elastic, and evolve heat; in both cases the muscular contents behave negatively as regards their electromotive force, in reference to the unaltered, living, resting substance. Hence he is inclined to regard a muscular contraction as a temporary, physiological, rapidly disappearing rigor. Rigor mortis is in a certain sense the last flickering act of a living muscle, [and he regards contraction as partial death of a muscle. But this is no explanation, and moreover there are important points of difference. We have no proof of a coagulum being formed during contraction, while the extensibility is increased during contraction and much diminished during rigor.]

Disappearance of Rigidity.—When rigor mortis passes off, there is a considerable amount of acid formed in the muscle, which dissolves the coagulated myosin. After a time **putrefaction** sets in, accompanied by the presence of micro-organisms and the evolution of ammonia and putrefactive gases (H_2S, N, CO_2—§ 184). [Hermann and Bierfreund attach much importance to the resolution of rigor mortis independently of putrefaction.]

According to Onimus, the **loss of excitability** which precedes the onset of rigor mortis occurs in the following order in man:—left ventricle, stomach, intestine (55 minutes); urinary bladder, right ventricle (60 min.); iris (105 min.); muscles of face and tongue (180 min.); the extensors

of the extremities (about one hour before the flexors); the muscles of the trunk (five to six hours). The œsophagus remains excitable for a long time (§ 325).

296. **MUSCULAR EXCITABILITY.**—By the term **excitability** or **irritability** of a muscle is meant that property of a muscle in virtue of which it responds to stimuli, at the same time becoming shorter and correspondingly thicker. The condition of excitement is the active condition of a muscle produced by the application of stimuli, and is usually indicated by the act of contraction. **Stimuli** are simply various forms of energy, and they throw the muscle into a state of excitement, while at the moment of activity the chemical energy of the muscle is transformed into work and heat, so that stimuli act as "**liberating**" or "**discharging forces.**" [These "discharging forces" may themselves be very feeble, but they are capable of causing the manifestation of the transformation of a large amount of energy.] The normal temperature of the body is most favourable for maintaining the normal muscular excitability; the excitability varies as the temperature rises or falls.

As long as the **blood-stream** within a muscle is uninterrupted, the first effect of stimulation of a muscle is to increase its energising power, partly because the circulation is more lively and the blood-vessels are dilated, but after a time, the energising power is diminished. Even in **excised muscles**, especially when the large nerve-trunks have already lost their excitability, the excitability is increased after a stimulus, so that the application of a series of stimuli of the same strength causes a series of contractions which are greater than at first (*Wundt*). Hence, we account for the fact that, although the first feeble stimulus may be unable to discharge a contraction, the second may, because the first one has increased the muscular excitability (*Fick*).

Effects of Cold.—If the muscles of a frog or tortoise be kept in a cool place, they may remain excitable for ten days, while the muscles of warm-blooded animals cease to be excitable after one and a half to two and a half hours. (For the heart, see § 55). A muscle, when stimulated *directly*, always remains excitable for a longer time when its motor nerve is already dead. Muscles just beginning to become dry exhibit excessive irritability.

[**Independent Muscular Excitability.**—Since the time of Albrecht v. Haller, and R. Whytt, physiologists have ascribed to muscle a condition of excitability which is entirely independent of the existence of motor nerves, but is dependent on certain constituents of the sarcous substance. Excitability, or the property of responding to a stimulus, is a widely distributed function of protoplasm or its modifications. A colourless blood-corpuscle or an amœba is excitable, and so are secretory and nerve-cells. In the first case, the application of a stimulus results in motion in an indefinite direction, in the second in the formation of a secretion, and in the third in the discharge of nerve-energy. In the case of muscle, a stimulus causes movement in a definite direction, called a contraction, and depending on the contractility of the sarcous substance. There are many considerations which show that *excitability is independent of the nervous system*, although in the higher animals, nerves are the usual medium through which the excitability is brought into action. Plants, however, are excitable, and they contain no nerves.]

Numerous experiments attest the "**independent excitability**" of muscle:—1. There are chemical stimuli, which do not cause movement when applied to motor nerves, but do so when they are applied directly to muscle; ammonia, lime water, carbolic acid. 2. The ends of the sartorius of the frog, in which no nerve-terminations (fig. 387) are observable by means of the microscope, contract when they are stimulated directly (*Kühne*). 3. Curare paralyses the extremities of the motor nerves, while the muscles themselves remain excitable (*Cl. Bernard*, *Kölliker*). The action of *cold*, or *arrest of the blood-supply* in an animal, abolishes the excitability of the nerves, but not of the muscles at the same time. 4. After section of its nerve, a muscle still remains excitable, even after the nerves have undergone

fatty degeneration (*Brown-Séquard, Bidder*). 5. Sometimes electrical stimuli act only upon the nerves and not upon the muscle itself (*Brücke*). [6. The fœtal heart contracts rhythmically before any nervous structures are discoverable in it.]

[**The Action of Curare.**—Curare, woorali, urari, or Indian arrow-poison of South America, is the inspissated juice of the Strychnos crevauxi. A watery extract of the drug, when injected under the skin or into the blood of an animal, acts chiefly upon the **motor nerve-endings**, and does not affect the muscular contractility. An active substance *curarin*, has been isolated from it (p. 589). Poison a frog by injecting a few milligrammes into the dorsal lymph-sac. In a few minutes after the poison is absorbed, the animal ceases to support itself on its fore-limbs; it lies flat on the table, its limbs are paralysed, and so are the respiratory movements in the throat. When completely under the action of the poison, the frog lies in any position, limp and motionless, neither exhibiting voluntary nor reflex movements. If the brain be destroyed and the skin removed, on faradising the sciatic nerve, no contraction of the muscle of the hind-limb occurs, but if the electrical stimulus be applied directly to the muscles, they contract, thus proving that curare poisons the **motor connections** and not the muscles. If the dose be not too large, the heart still continues to beat, and the vaso-motor nerves remain active.]

[**Methods.**—(1) **Local Application.**—Bernard took two nerve-muscle preparations, put some solution of curare into two watch-glasses, and dipped the nerve into one glass and the muscle of the other preparation into the other glass. The curare penetrated into both preparations, and he found, on stimulating the nerve which had been steeped in curare, that its muscle still contracted, so that the curare had not acted on the motor nerve-fibres; while stimulation of the nerve of the other preparation produced no contraction, although the corresponding muscle contracted. In the latter case, the curare had penetrated into the muscle and affected the **intra-muscular portions of the nerve.**]

[(2) But it is the terminal or **intra-muscular portions** of the nerves, not the nerve-trunk, which are paralysed. Ligature the sciatic artery, or, better still, tie all the parts of the hind-limb of a frog, except the sciatic nerve, at the upper part of the thigh (fig. 384). Inject curare into the dorsal lymph-sac. The poisoned blood will, of course, circulate in every part of the body except the ligatured limb. The shaded parts are traversed by the poison. The animal can still, at a certain stage of the poisoning, pull up the non-poisoned limb, while it cannot move the poisoned one. At this time, although poisoned blood has circulated in the sacral and intra-abdominal parts of the nerves, yet they are not paralysed, so that the poison does not act on this part of the trunk of the nerve. But we can show that it does not act on any part of the extra-muscular trunk of the nerve. This is done by ligaturing the arteries going to the gastrocnemius muscle, and then poisoning the animal. On stimulating the nerve on the ligatured side, the gastrocnemius of that side contracts, although the whole length of the nerve-trunk was supplied by poisoned blood. Therefore it is the *intra-muscular terminations* of the nerves which are acted on.]

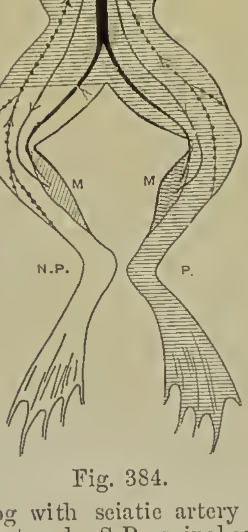


Fig. 384.

Frog with sciatic artery ligatured. S.P., spinal cord with afferent and efferent nerves; P., poisoned, N.P., non-poisoned leg; M, gastrocnemius muscles.

[By means of the following arrangement we may prove that the terminal parts of the nerve are paralysed. Ligature the sciatic artery of one leg of a frog, and then inject curare into a lymph-sac. After the animal is fully poisoned, expose the sciatic nerve in both legs, leaving all the muscles below the knee-joint, then clean and divide the femur at its middle. Pin a straw flag to each limb, and fix both femora in a clamp, with the gastrocnemii uppermost, as in fig. 385. Place the two nerves, N, on electrodes attached to two wires coming from a commutator, C (fig. 385). From the opposite

binding-screws of the commutator, two wires pass to the gastrocnemii. The other two binding-screws of the commutator are connected with the secondary coil of an induction machine (§ 330). The bridge of the commutator can be turned so as to pass the current either through both muscles or both nerves—the latter is the case in the diagram (H). When *both nerves* are stimulated, only the *non-poisoned leg* (NP) contracts. Reverse the commutator, and pass the current through *both muscles*, when *both contract.*]

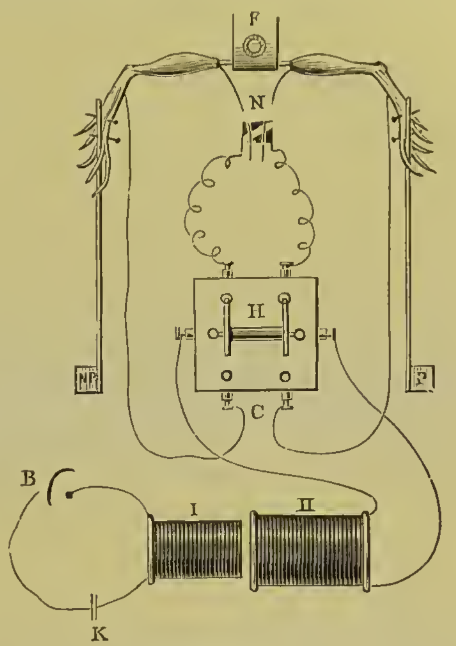


Fig. 385.

Scheme of the curare experiment. B, battery ; I, primary, II, secondary spiral ; N, nerves ; F, clamp ; NP, non-poisoned leg ; P, poisoned leg ; C, commutator ; K, key.

[**Rosenthal's Modification.**—Push the secondary coil far away from the primary, and pass the current through both muscles. Gradually approximate the secondary to the primary coil, and in doing so it will be found that the non-poisoned leg contracts first, but on continuing to push up the secondary coil, both limbs contract. Thus, the poisoned limb does not respond to so feeble a faradic stimulus as the non-poisoned one, a result which is not due to the action of the curare on the excitability of the muscle. The non-poisoned limb responds to a feebler stimulus because its motor nerve terminations are not paralysed while the poisoned leg does not do so, because the motor terminations are paralysed. A feebler induced shock suffices to cause a muscle to contract when it is applied to the nerve, than when it is applied to the muscle itself directly. In large doses curare also affects the spinal cord (p. 589).]

[**On what structures does curare act?**—These experiments prove that curare does not paralyse the motor nerve-trunks, nor the muscular fibres, and that it acts on the motor terminations within the muscles, but they do not enable us to state the precise part of the nerve-ending so affected. It may act on (1) the nerve just before it pierces the sarcolemma,

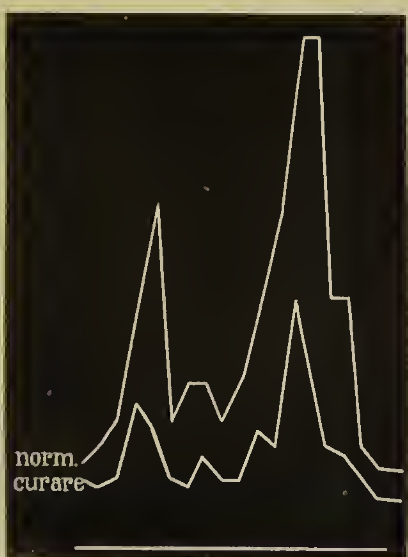


Fig. 386.

Fig. 387.

Fig. 386.—Curve showing the excitability in the sartorius of a frog in a normal and curarised muscle. Fig. 387.—Distribution of nerves in the sartorius of a frog and the curve of excitability in different parts of the muscle, *i.e.*, the excitability is greatest where there are most nerve-endings, and lowest where there are none.

(2) the sub-lemmar axis-cylinder, (3) the end-plates, (4) the terminal branches or spray. Kühne and Pollitzer have made it probable that, even when a muscle is thoroughly impregnated with

curare, some of the nervous apparatus is unaffected. The sartorius is most excitable where there are most nerves (fig. 387), and even in a muscle profoundly poisoned with curare, the distribution of excitability varies with the number of nerves in the several parts of the muscle (fig. 386) just as in a normal muscle, with this difference, that the excitability of all the parts of the muscle containing nerves is less than normal. That this variation in excitability is due to nervous structures is shown by using a polarising anelectrotonic current (§ 335), which depresses the excitability of nerve-fibres, and then this difference of excitability disappears, the curve of excitability running parallel with the abscissa, so that the difference does not seem to be due to purely muscular causes.]

[Pollitzer, speculating as to which part of the terminal nerve is affected, supposes that all parts beyond the last node of Ranvier retain their functions, and he supposes that it is not the axis-cylinders themselves, but the cement at the nodes, on which the drug exerts its specific action.]

Neuro-Muscular Cells.—Even in the lower animals, *e.g.*, Hydra and Medusæ, there are unicellular structures called "*neuro-muscular cells,*" in which the nervous and muscular substances are represented in the same cell (*Kleinenberg and Eimer*). [This view, however, is very doubtful; the outer part of these cells is adapted for the action of stimuli, and corresponds to the nervous receptive organ, while the inner deeper part is contractile, and is the representative of the muscular part.]

Muscular Stimuli.—Various stimuli cause a muscle to contract, either by acting upon its motor nerve, or upon the muscular substance itself (§ 324). [The former is called **indirect stimulation**, the latter **direct stimulation.**]

1. Under ordinary circumstances, the **normal stimulus** exciting a muscle to contract is the **nerve impulse** which passes along a nerve, but its exact nature is unknown.

2. **Chemical Stimuli.**—All chemical substances which alter the chemical composition of a muscle with sufficient rapidity act as *muscular stimuli.* Mineral acids (HCl 0·1 per cent.), acetic and oxalic acids, the salts of iron, zinc, copper, silver, and lead, bile, all act in weak solutions as muscular stimuli; they act upon the motor nerve only when they are more concentrated. Lactic acid and glycerin, when concentrated, excite only the nerve; when dilute, only the muscle. [The lower end of the sartorius, which contains no nerves, may be dipped into glycerin, and it will not contract, but if it be dipped deeper to where there are nerve-endings, it will contract at once.] Neutral alkaline salts act equally upon nerve and muscle; alcohol and ether act on both very feebly. When water is injected into the blood-vessels, it causes fibrillar muscular contractions (*v. Wittich*), while a 0·6 per cent. solution of NaCl may be passed through a muscle for days without causing contraction (*Kölliker, O. Nasse*). [Carslaw, under Ludwig's direction, however, found that solutions containing 0·5 to 0·2 per cent. NaCl, when perfused through the muscles of a frog, excite many short, powerful attacks of tetanus, separated from each other by periods of rest. Solutions containing 0·5 to 0·7 per cent. NaCl, *i.e.*, so-called "indifferent fluids" or "normal saline," are not without influence, but of all known saline solutions, they injure a nerve-muscle preparation least. Solutions of 1 to 2 per cent. rapidly kill the muscle.] Acids, alkalies, and extract of flesh diminish the muscular excitability, while the muscular stimuli, in small doses, increase it (*Ranke*). *Gases* and *vapours* stimulate muscle; they cause either a simple contraction (*e.g.*, HCl), or at once permanent contraction or contracture (*e.g.*, Cl). Long exposure to the gas causes rigidity. The vapour of bisulphide of carbon stimulates only the *nerves*, while most vapours (*e.g.*, HCl) kill without exciting them (*Kühne and Jani*).

Method.—In making experiments upon the chemical stimulation of muscle, it is inadvisable to dip the transverse section of the muscle into the solution of the chemical reagent (*Hering*). The chemical stimulus ought to be applied in solution to a limited portion of the uninjured surface of the muscle; after a few seconds we obtain a contraction or fibrillar twitchings of the superficial muscular layers (*Hering*).

[**Rhythmical Contraction.**—While rhythmical contractions are very marked in smooth muscle, (especially if it is stretched or subjected to considerable internal pressure, as in the hollow viscera), *e.g.*, the intestine, uterus, ureter, blood-vessels, and also in the striped but involuntary

cardiac musculature (§ 58), they are not, as a rule, very common in striped voluntary muscle. Chemical stimuli are particularly effective in producing them.] If the sartorius of a curarised frog be dipped into a solution composed of 5 grms. NaCl, 2 grms. alkaline sodium phosphate, and 0·5 grm. sodium carbonate in 1 litre of water, at 10° C., the muscle contracts rhythmically, and may do so for several days, especially with a low temperature (*Biedermann*). This recalls the rhythmical contraction of the heart. [Kühne found a similar result. The rhythm is arrested by lactic acid and restored by an alkaline solution of NaCl.] Rhythmical movements may also be induced in the sartorius (frog), by the combined action of a dilute solution of sodic carbonate and an ascending constant electrical current. Compare also the action of a constant current on the heart (§ 58).

3. **Thermal Stimuli.**—If an excised frog's muscle be rapidly heated to 28° C., a gradually increasing contraction occurs, which, at 30° C., is more pronounced, reaching its maximum at 45° C. If the temperature be raised, "**heat-stiffening**" rapidly ensues. The *smooth* muscles of warm-blooded animals also contract when they are warmed, but those of cold-blooded animals are elongated by heat (*Grünhagen*). If a frog's muscle be cooled to 0°, it is very excitable to mechanical stimuli (*Grünhagen*); it is even excited by a temperature under 0° (*Eckhard*).

Cl. Bernard observed that the muscles of animals, artificially cooled, remained excitable many hours after death (§ 225). Heat causes the excitability to disappear rapidly, but increases it temporarily.

4. **Mechanical Stimuli.**—Every kind of sudden mechanical stimulus, provided it be applied with sufficient rapidity to a muscle (and also to a nerve), causes a *contraction*. If stimuli of sufficient intensity be repeated with sufficient rapidity, *tetanus* is produced. *Strong local* stimulation causes a weal-like, long-continued contraction at the part stimulated (§ 297, 3, *a*). Moderate tension of a muscle increases its excitability.

5. **Electrical Stimuli** will be referred to when treating of the stimulation of nerve (§ 324).

Other Actions of Curare.—When it is injected into a frog, either into the blood or subcutaneously, it causes at first paralysis of the *intra-muscular ends of the motor nerves* (p. 586), while the muscles themselves remain excitable. The sensory nerves, the central nervous system, viscera, heart, intestine, and the blood-vessels are not affected at first (*Cl. Bernard, Kölliker*). [If the skin be stimulated, the frog pulls up the ligatured leg reflexly, although the other leg remains quiescent; this shows that the **sensory nerve** and **nerve-centres** are still intact; but when the action of the drug is fully developed, no amount of stimulation of the skin or the posterior roots of the nerves will give rise to a reflex act, although the motor nerve of the ligatured limb is known to be excitable; hence it is probable that the nerve-centres in the cord themselves are ultimately affected. If the dose be very large, the heart and blood-vessels are affected.] In **warm-blooded animals** death takes place by **asphyxia**, owing to paralysis of the diaphragm, but of course there are no spasms. In **frogs**, where the skin is the most important respiratory organ, if a suitable dose be injected subcutaneously, the animal may remain motionless for days and yet recover, the poison being eliminated by the urine (*Kühne*). If the dose be large, the inhibitory fibres of the vagus may be paralysed. In electrical fishes, the sensory nerves, and in frogs, the lymph-hearts, are paralysed. A dose sufficient to kill a frog, when injected under its skin, will not do so if administered by the mouth, because the poison seems to be eliminated as rapidly by the kidneys as it is absorbed from the gastric mucous membrane. For the same reason the flesh of an animal killed by curare is not poisonous when eaten. If, however, the ureters be tied, the poison collects in the blood, and poisoning takes place (*L. Hermann*). [In this case the mammal may exhibit convulsions. Why? Curare paralyses the respiratory nerves, so that asphyxia is produced from the venosity of the blood. It affects the respiratory nerve-endings before those in the muscles generally, so that when the venous blood stimulates the nerve-centres, the partially affected muscles respond by convulsions. Other narcotics may excite convulsions indirectly by inducing a venous condition of the blood, while the motor centres, nerves, and muscles are still unaffected.] Large doses, however, poison uninjured animals even when given by the mouth. The nerves and muscles of poisoned animals exhibit considerable electromotive force. [For the effect of curare on lymph-formation (§ 199, 6).]

Atropin appears to be a specific poison for **smooth muscular tissue**, but different muscles are differently affected (*Szpilmann, Luchsinger*). [This is doubtful. A small quantity of atropin seems to affect motor nerves of smooth muscle in the same way that curare does those of striped muscle; we must remember, however, that there are no end-plates proper in the former, so that the link between the nerve-fibrils and the contractile substance is probably different in

the two cases. It is well known that the amount of striped and smooth muscle varies in the œsophagus in different animals. Szpilmann and Luchsinger found that, after the action of atropin, stimulation of the peripheral end of the vagus will still cause contraction of the striped muscular fibres in the œsophagus, but not of the smooth fibres, although both forms of muscular tissue respond to direct stimulation.]

After section of the motor nerve of a muscle, the excitability undergoes remarkable changes; after three to four days the excitability of the paralysed muscle is diminished, both for direct and indirect stimuli (p. 588); this condition is followed by a stage during which a constant current is more active than normal, while induced currents are scarcely or not at all effective (§ 339, I.). The excitability to mechanical stimuli is also increased. The increased excitability occurs until about the seventh week; it gradually diminishes until it is abolished towards the sixth to the seventh month. Fatty degeneration begins in the second week after section of the motor nerve, and goes on until there is complete muscular atrophy. Immediately after section of the sciatic nerve, Schmulewitsch found that the excitability of the muscles supplied by it was increased.

297. **CHANGES IN A MUSCLE DURING CONTRACTION.—I. Phenomena visible to the naked eye.**—1. When a muscle contracts, it becomes **shorter** and at the same time correspondingly **thicker**.

The degree of contraction, which in very excitable frogs may be 65 to 85 per cent. (72 per cent. mean) of the total length of the muscle, depends upon various conditions:—(*a*) Up to a certain point, increasing the **strength of the stimulus** causes a greater degree of contraction; (*b*) as the **muscular fatigue** increases, *i.e.*, after continued vigorous exertion, the stimulus remaining the same, the extent of contraction is diminished; (*c*) the **temperature** of the surroundings has a certain effect. The extent of the contraction is increased in a frog's muscle—the strength of stimulus and degree of fatigue remaining the same—when it is heated to 33° C. If the temperature be increased above this point, the degree of contraction is diminished (*Schmulewitsch*).

2. The **volume** of a contracted muscle is slightly diminished (*Swammerdam*,† 1680). Hence, the **specific gravity** of a contracted muscle is slightly increased, the ratio to the non-contracted muscle being 1062 : 1061 (*Valentin*); the diminution in volume is, however, only $\frac{1}{1370}$ although this has recently been denied by J. Ewald.

Methods.—(*a*) Erman placed portions of the body of a live eel in a glass vessel filled with an indifferent fluid. A narrow tube communicated with the glass vessel, and the fluid rose in the tube to a certain level. As soon as the muscles of the eel were caused to contract, the fluid in the index-tube sank. (*b*) Landois demonstrates the decrease in volume by means of a manometric flame. The cylindrical vessel containing the muscle is provided with two electrodes fixed into it in an air-tight manner. The interior of the vessel communicates with the gas supply, while there is a small narrow exit-tube for the gas, which is lighted. Every time the muscle contracts the flame diminishes. The same experiment may be performed with a contracting heart.

3. **Total and Partial Contraction.**—Normally, all stimuli applied to a muscle or its motor nerve cause contraction in all its muscular fibres. Thus the muscle conducts the state of excitement to all its parts. Under certain circumstances, however, this is not the case, viz.:—(*a*) when the muscle is greatly *fatigued*, or when it is about to die, *violent mechanical* stimuli, as a vigorous tap with the finger or a percussion hammer (and also chemical or electrical stimuli), cause a localised contraction of the muscular fibres. This is Schiff's "**idio-muscular contraction.**" The same phenomenon is exhibited by the muscles of a healthy man, when the blunt edge of an instrument is drawn transversely over the direction of the muscular fibres. (*b*) Under certain as yet but imperfectly known conditions, a muscle exhibits so-called **fibrillar contractions**, *i.e.*, short contractions occur alternately in different bundles of muscular fibres. This is the case in the muscles of the tongue, after section of the hypoglossal nerve; and in the muscles of the face, after section of the facial nerve (§ 349, 4).

[In some phthisical patients there is marked muscular excitability, so that if the pectoral muscle be percussed, a local contraction—idio-muscular—occurs, either confined to the spot, or two waves may proceed outwards and return to the spot struck.]

Cause of Fibrillar Contraction.—According to Bleuler and Lehmann, section of the hypo-

glossal nerve in rabbits is followed by fibrillar contractions after sixty to eighty hours; these contractions may continue for months, even when the divided nerve has healed and is stimulated above the cicatrix so as to produce movements in the corresponding half of the tongue. Stimulation of the lingual nerve increases the fibrillar contractions or arrests them. This nerve contains vaso-dilator fibres derived from the chorda tympani. Schiff is of opinion that the increased blood-stream through the organ is the cause of the contractions. Sig. Mayer found that, by compressing the carotids and subclavian, and again removing the pressure so as to permit free circulation, the muscles of the face contracted. Section of the motor nerves of the face did not abolish the phenomenon, but compression of the arteries did. The cause of the phenomenon, therefore, seems to lie within the muscles themselves. This phenomenon may be compared to the *paralytic secretion* of saliva and pancreatic juice which follows section of the nerves going to these glands (pp. 249, 309). Similar fibrillar contractions occur in man under pathological conditions, but they may also occur without any signs of pathological disturbance. [Fibrillar contractions, due to a central cause, occur in monkeys after excision of the thyroid gland (§ 103, III.). Some **drugs** cause fibrillar muscular contractions, *e.g.*, aconitin, guanidin, nicotin, pilocarpin, but physostigmin produces them in warm-blooded animals (not in frogs). According to Brunton these drugs probably act by **irritating** the **motor nerve-endings**, as the contractions are gradually abolished by curare.]

II. Microscopic Phenomena.—1. Single muscular *fibrillæ* exhibit the same phenomena as an entire muscle, in that they contract and become thicker. 2. There is great difficulty in observing the changes that occur in the individual parts of a muscular fibre during the act of contraction. This much is certain, that the muscular elements become shorter and broader during contraction, and that the transverse striæ approach nearer to each other (*Bowman*, 1840). 3. There is great difference of opinion as to the behaviour of the doubly refractive (anisotropous) and the singly refractive media.

Engelmann's View.—Fig. 388, 1, represents a passive muscular element—from *c* to *d* is the **doubly refractive contractile substance**, with the median disc, *a*, *b*, in it; *h* and *g* are the lateral discs. Besides these, in each of the singly refractive discs there is a *clear* disc—"secondary disc," *f* and *e*, which is only slightly doubly refractive. This occurs only in the muscles of insects. Fig. 1, on the *right*, shows the same element in polarised light, whereby the middle area of the element, as far as the contractile substance proper extends, is, owing to its double refraction, bright; while the other part of the muscular element, owing to its being singly refractive, is black. Fig. 388, 2, is the transition stage, and 3 the proper stage of contraction of the muscular element. In both cases the figures on the *left* are viewed in ordinary light, and on the *right*, in polarised light. According to Engelmann, during contraction (fig. 388, 3), the singly refractive disc becomes as a whole more refractive, the doubly refractive less so. Consequently, a fibre at a certain degree of contraction (2), when viewed in *ordinary* light, may appear homogeneous and but slightly striped transversely = the **homogeneous** or **transition stage**. During a greater degree of contraction (3), very dark transverse stripes reappear, corresponding to the singly refractive discs. At every stage of the contraction, as well as in the transition stage, the singly and doubly refractive discs are sharply defined, and are recognised by the polariscope as regular alternating layers (in 1, 2, and 3 on the right). These do not change places during the contraction. The height of both discs is diminished during contraction, but the singly refractive do so more rapidly than the doubly refractive discs. The total volume of each element does not undergo any appreciable alteration in volume during the contraction. Hence, the doubly refractive discs increase in volume at the expense of the singly refractive. From this it is concluded that, during the contraction, fluid passes from the singly refractive into the doubly refractive discs; the former shrink, the latter swell.

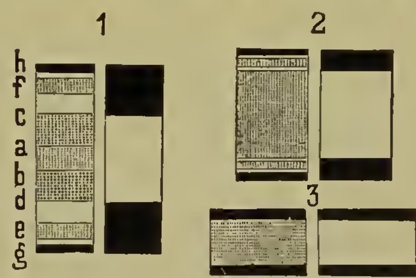


Fig. 388.
The microscopic appearances during a muscular contraction in the individual elements of the fibrillæ. 1, 2, 3 (after *Engelmann*).

[If a living portion of an insect's muscle be examined in its own juice, contraction-waves may be seen to pass over the fibres. When a contraction-wave passes over part of the fibres, the discs become *shorter* and *broader*; at the same time, in the fully contracted part, the dim disc appears lighter than the centre of the light disc. There is said to be a "reversal of the stripes" from what obtains in a passive muscle. Before this stage is reached, there is an intermediate stage where the two bands are almost uniform in appearance. According to Ranvier, however, who has examined the muscles of the retro-lingual membrane of the frog (p. 564),

when a muscular fibre contracts, the stripes do not disappear nor are they reversed; the dim disc alone appears to be contractile, and it becomes shorter and broader. This disc, as it were, strives to assume a form with the smallest surface, *i.e.*, to become spherical.]

Methods.—These phenomena are best observed by "fixing" the different stages of rest or contraction, by suddenly plunging the muscular fibrillæ of insect's muscles into alcohol or osmic acid, which coagulates the muscle-substance. The actual contraction may be observed under the microscope in the transparent parts of the larvæ of insects.

Diffraction Spectrum.—A thin muscle, *e.g.*, the sartorius of the frog, when placed directly behind a narrow slit running at right angles to the course of the fibres, yields a **diffraction-spectrum.** When the muscle contracts, as by mechanical stimulation, the spectrum broadens, a proof that the interspaces of the transverse stripes become narrower (*Ranvier*).

298. MUSCULAR CONTRACTION. — Methods. — In order to determine the duration of each phase of a muscular contraction, **myographs** of various forms are used.

V. Helmholtz's Myograph is shown in fig. 389. A muscle, M—say the gastrocnemius of a frog attached to the femur—is fixed by the femur in a clamp, K; its lower end is attached to a movable lever carrying a scale-pan and weight, W, the weight being varied at pleasure. When the muscle contracts, necessarily it raises the lever. At the free end of the lever is a movable style, F, which inscribes its movements on a revolving cylinder caused to rotate at a uniform rate by means of clock-work. The cylinder is covered with smoked enamelled paper in the flame of a turpentine lamp.

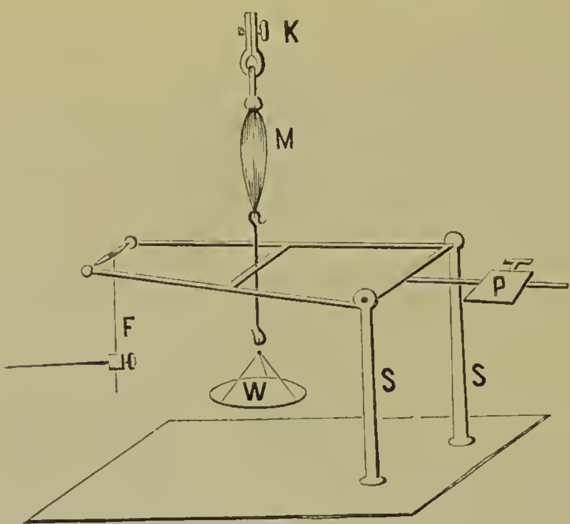


Fig. 389.

Scheme of v. Helmholtz's myograph. M, muscle fixed in a clamp, K; F, writing style; P, weight or counterpoise for the lever; W, scale-pan for weights; S, S, supports for the lever.

When the muscle contracts, it inscribes a curve—the "**muscle-curve,**" or "**myogram.**" The **abscissa** of the curve indicates the **duration** of the contraction, but of course the rate at which the cylinder is moving must be known. The **ordinates** represent the **height** of contraction at any particular part of the curve.

The muscle-curve may be inscribed upon a smoked glass plate attached to one limb of a vibrating tuning-fork. Such a curve registers the time-units in all its parts. Suppose each vibration of the tuning-fork = 0·01613 second, then the duration of any part of such a curve is obtained by counting the number of vibrations and multiplying by 0·01613 second.

[**Fick's Pendulum Myograph.**—A board fixed to the wall carries a heavy iron **pendulum**, P, whose axis, A, A, moves on friction rollers (fig. 390). At the lower swinging end are two glass plates, G and G′ fixed to a bearer, T. The plates can be adjusted by means of the screw, *s*, so that several curves can be written one above the other. The plate, G′, on the posterior surface is merely a compensator, so that, when G is elevated, G′ is lowered, and thus the duration of the oscillation is not altered. The **spring catches**, H, H, which can be turned inwards or outwards, are used to fix the pendulum by the teeth, *a*, *a*, when it is drawn to one side. The pendulum is drawn to one side and fixed, *a*, in H, so that when H is pulled down, it is liberated and swings to the other side, where it is caught by the detent H at the opposite side. In the improved form, the catches, H, are made to slide along a rod like the arc of a circle, so that the length of the swing can be varied. As the pendulum swings from one side to the other, the projecting points, *a*, *a*, knock over the **contact key**, *b*, and the current is opened and a shock transmitted to the muscle. The **writing lever** to which the muscle is attached is usually a heavy one, and a style writes upon the smoked surface of the glass. Of course, when the pendulum swings, it moves with unequal velocities at different parts of its course.]

[When using the pendulum myograph to study a muscular contraction, arrange it as in fig. 392. The frog's muscle is attached to a writing lever, which is very like the lever in fig. 390, while the style inscribes its movements on the blackened plate.]

[The pendulum is fixed in the catch, C, as shown in the figure; the key, K′, is closed and placed in the primary circuit, while two wires from the secondary coil of an induction machine are attached to the muscle. When the pendulum swings, the projecting tooth, S, knocks over the contact at K′, and breaks the primary circuit, when a shock is instantly transmitted through the muscle. Before stimulating, allow the pendulum to swing to obtain an abscissa. The time is recorded by a vibrating tuning-fork, of known rate of vibration, connected with a Dupré's electric chronograph. Dupré's chronograph is merely a small electro-magnet with a fine writing-style attached, which vibrates when it is introduced in an electrical circuit, in which is placed a vibrating tuning-fork. The signal vibrates just as often as the tuning-fork.]

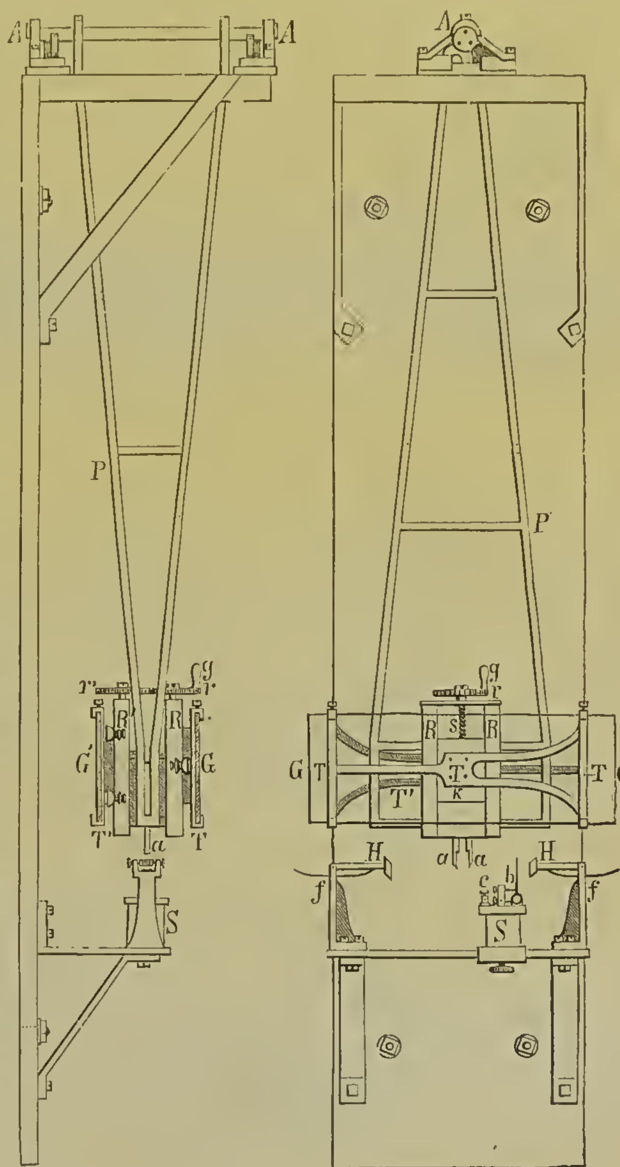


Fig. 390.

Fick's pendulum myograph, as improved by v. Helmholtz ($\frac{1}{12}$ natural size,) side and front view.

[**Du Bois-Reymond's Spring Myograph.**—It consists of a glass plate fixed in a frame, and moving on two polished steel wires, stretched between the supports A and B (fig. 393). At *b* is a spring which, when it is compressed between the upright, B, and the knob, *b*, drives the glass plate from B to A. As the plate moves from one side to the other, a small tooth, *d*, on its under surface, opens the key, *h*, and thus a shock is transmitted to the muscle. The arrangement otherwise is the same as for the pendulum myograph. The smoked glass plate is liberated by the projecting finger plate attached to the upright, A.]

[**Marey's Simple Myograph.**—The gastrocnemius is attached to a horizontal lever, which inscribes its movements on a revolving cylinder. This form of myograph, when provided with two levers, is very useful for comparing the action of a poison on one limb, the other being unpoisoned.]

Pflüger's stationary form is simply a Helmholtz's myograph (fig. 389) arranged to record its movements on a stationary glass plate, so that the muscle merely makes a vertical line or ordinate instead of a curve; it thus merely indicates the height or extent of the contraction, not its duration.]

A **rapidly rotating disc** was used by Valentin and Rosenthal for registering the muscle-curve, while Harless used a plate which was allowed to fall rapidly, the so-called "**Fall-myograph.**" In all these experiments it is necessary to indicate at the same time the moment of stimulation.

[**Moist-Chamber.**—In studying the contraction of a muscle it should be kept under conditions as normal as possible. This is effected by suspending it in a moist-chamber (fig. 391), the air of which is kept moist by means of a piece of blotting-paper moistened with normal saline.]

Contraction-Curve of Human Muscle.—In man, another principle is adopted, viz., to measure the increase in **thickness** during the contraction, either by means of a lever or a compressible tambour, such as is used in Brondgeest's pansphygmograph (fig. 88). The *thickening* of the abductor muscles of the thumb may be registered by means of Marey's **pince myographique** (fig. 409).

I. Simple Contraction.—If a **single induction shock** *or stimulus of momentary duration* be applied to a muscle, a "**simple muscular contraction**," [or shortly, a *contraction* or **twitch**] is the result, *i.e.*, the muscle rapidly shortens and quickly returns again to its original relaxed condition.

Muscle-Curve or Myogram.—Suppose a single stimulus be applied to a muscle attached to a light writing-lever, which is not "over-weighted" with any weight attached to it, then, when the muscle contracts, the following events take place:—

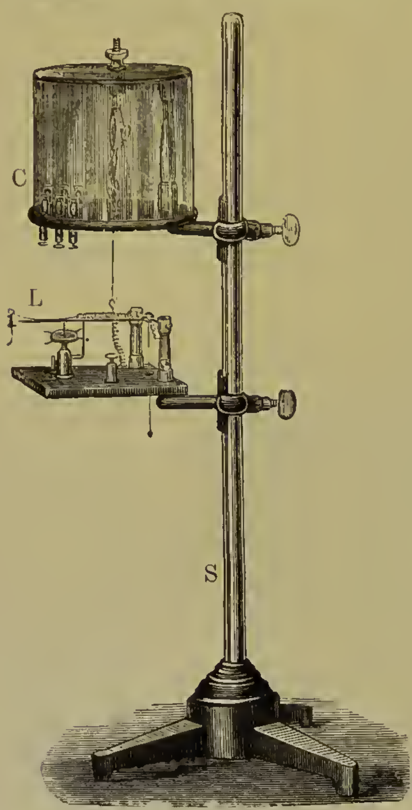


Fig. 391.
A muscle chamber, C, for a frog's muscle, the latter attached to Tigerstedt's recording lever, and the whole supported on a stand, S. (Made by Petzold of Leipzig.)

[(1) A period or stage of latent stimulation (figs. 394, 396).
(2) A period of increasing energy or contraction.
(3) A period of decreasing energy or more rapid relaxation.
(4) A period of slow relaxation, or the elastic after-vibration.]

The muscle-curve proper is composed of 2, 3, and 4.

(1). **The latent period** (fig. 394, *a*, *b*) consists in this, that the muscle does not begin to contract precisely at the moment the stimulus is applied to it, but the contraction occurs somewhat *later*, *i.e.*, a short, but measurable interval, elapses between the application of a momentary stimulus and the contraction (*v. Helmholtz*). If the entire muscle be stimulated by a momentary stimulus, *e.g.*, a **single break induction shock** is found; the duration of the latent period is about 0·01 second [*i.e.*, when the muscle records its movements by means of a lever attached to the muscle]. In smooth muscle, the latent period may last for several seconds.

[Although no change be visible in a muscle during the latent period, nevertheless it has been held until quite recently that some change does take place within the muscle-substance, and it was maintained that the electrical current of the muscle is diminished during this period, or we have what is known as the **negative variation** of the muscle-current (*Bernstein*—§ 333).] [The recent careful experiments, however, of Burdon-Sanderson on frogs' muscles, where the moment of stimulation, the electromotive changes (determined by a capillary electrometer), and the change of muscular form, were all recorded simultaneously by photographic means, show that the electrical movement or response, instead of preceding the mechanical change of form of the muscle, actually accompanies the latter (fig. 395). The theory, therefore, that the electrical variation precedes the actual muscular contraction and occurs during the latent period must be abandoned. Burdon-Sanderson has also shown that there is a true latent period in muscle which may be as short as $2\frac{1}{2}$ thousands of a second $= \frac{1}{400}$ sec., *i.e.*, $\frac{1}{400}$ second elapses in a frog's muscle between the stimulation and the first sign of change of form in the muscle.]

In **man**, the latent period varies between 0·004 and 0·01 second. If the experiment be so arranged that the muscle can contract as soon as the stimulus is applied to it, *i.e.*, before time is lost in making the muscle tense; or to put it otherwise, if the muscle has not "to take in slack," as it were, the latent period may fall below 0·004 second (*Gad*). If the muscle be still

attached to the body, protected as much as possible from external influences and properly supplied with blood, the latent period may be reduced to 0·0033 or even 0·0025. [All these results have reference to curves recorded graphically. It is important to notice how the time is shortened when the record is taken by photographic means as mentioned above.]

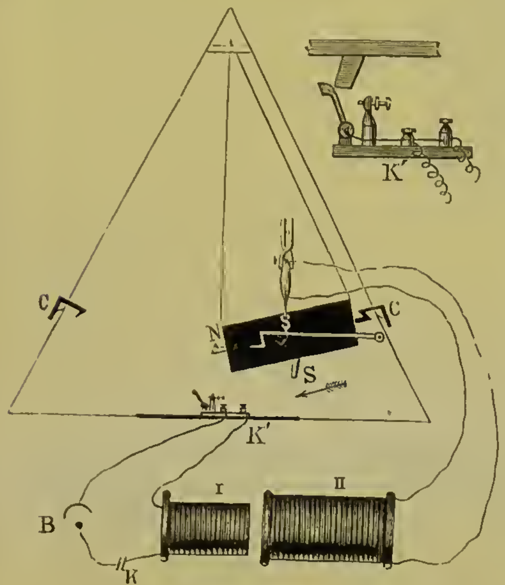


Fig. 392.

Scheme of the arrangement of the pendulum myograph. B, battery; I, primary, II, secondary spiral of the induction machine; S, tooth; K′, key; C, C, catches or detents; K′ in the corner, scheme of K′; K, key in primary circuit. The short-circuiting key in the secondary circuit is omitted.

Influences modifying the latent period.—The latent period is shortened by an increased strength of the stimulus and by heat; while fatigue, cooling, and increasing weight lengthen it (*Lauderbach, Mendelssohn, Yeo, Cash*). The latent period of a break-contraction is longer than that of a make-contraction. The red muscles have a longer latent period than the white. Before the muscle contracts as a whole, the individual fibres within it must have contracted. We must, therefore, conclude that the latency of the individual muscular elements is shorter than that of the entire muscle (*Gad, Tigerstedt*).

(2). **The contraction** or **stage of increasing energy**, *i.e.*, from the moment the muscle begins to shorten until it reaches its greatest degree of contraction (*b d*). At first the muscle contracts slowly, then more rapidly, and again more slowly, so that the ascending limb of the curve has somewhat the form of an *f*. This stage lasts 0·03 to 0·04 second. It is shorter when the contraction is shorter (weak stimulus) and the less the weight the muscle has to lift. It also varies with the excitability of the muscle, being shorter in a fresh, non-fatigued muscle.

(3). **Elongation** or **stage of decreasing energy.**—After the muscle has con-

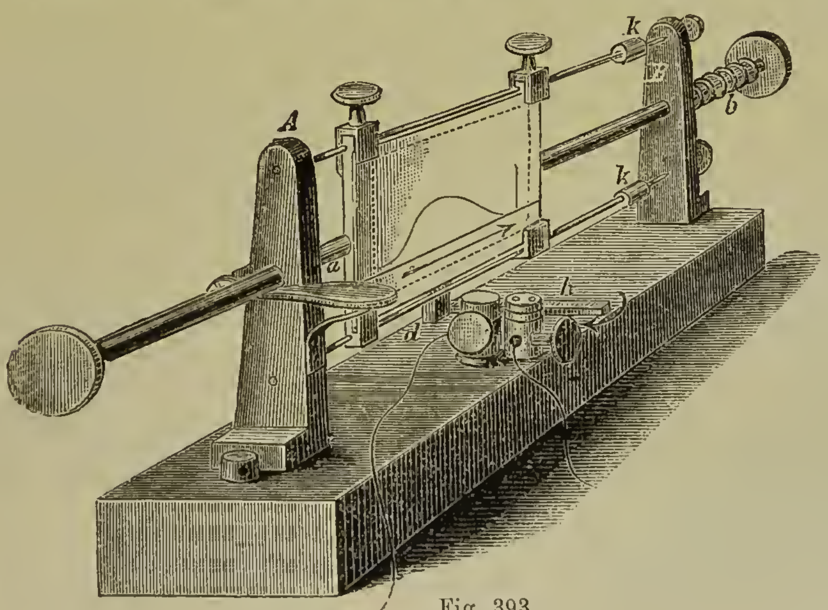


Fig. 393.

Spring myograph or "shooter."

tracted up to its maximum for any particular stimulus, it begins to relax—at first slowly, then rapidly—and lastly more slowly, so that an inverse of an *f* is obtained

(*d e*). This stage is usually of shorter duration than (2). The duration varies with the strength of the stimulus, being shorter than (2) with a weak stimulus, and longer with a strong stimulus. It also depends upon the extent to which the muscle is loaded during contraction.

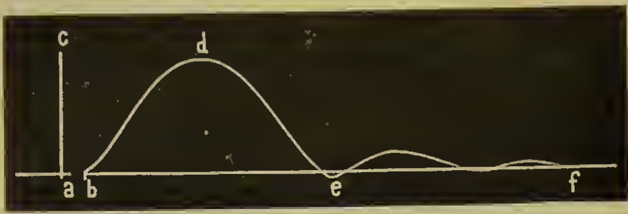


Fig. 394.

Muscle-curve produced by a single induction shock applied to a muscle. *a–f*, abscissa; *a–c*, ordinate; *a b*, period of latent stimulation; *b d*, period of increasing energy; *d c*, period of decreasing energy; *c f*, elastic after-vibrations.

(4). The fourth stage has received various names—**stage of elastic after-vibration** [**residual contraction** or **contraction remainder** (*Hermann*). The after-vibrations (*e f*), which disappear gradually, depend upon the elasticity of the muscle. The duration of this stage is longest with a

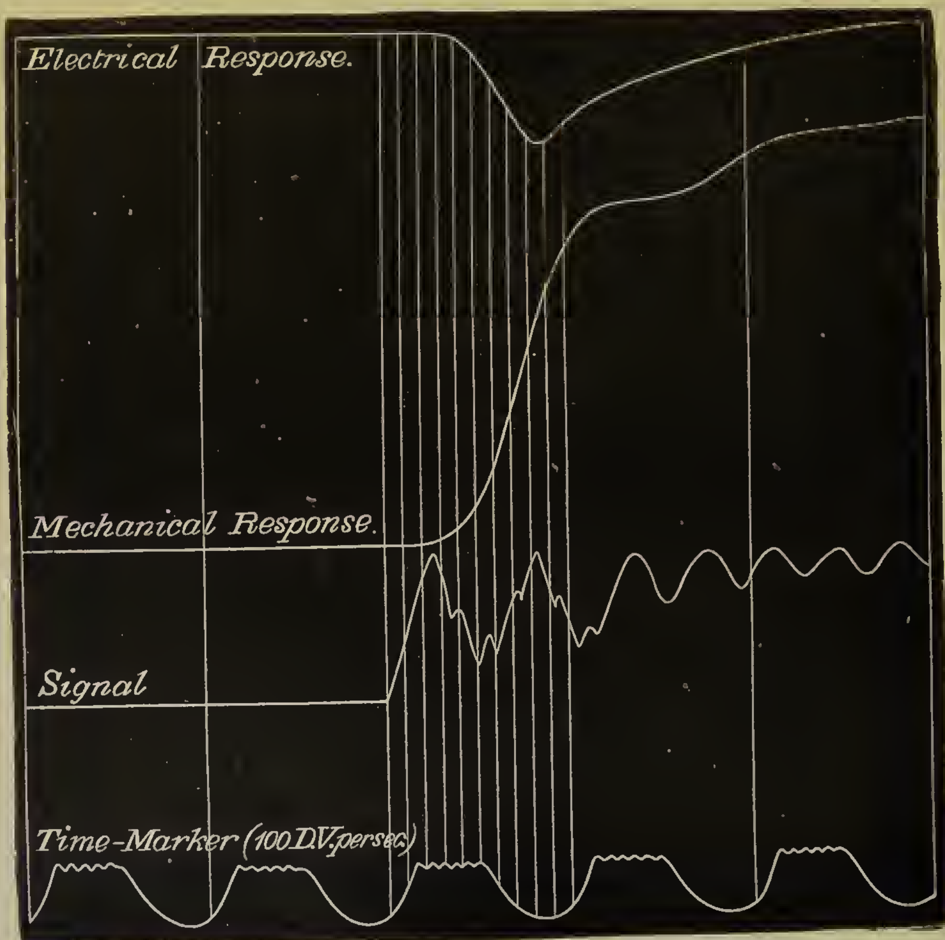


Fig. 395.

Electrical response = the sudden negativity and the subsequent relative positivity of the muscular surface of the gastrocnemius stimulated indirectly. Mechanical response = the beginning of the change of form of the part of the muscle stimulated directly; signal = the distance of the ordinates from each other = $\frac{1}{1000}$ second. The rise of the line indicates the moment of opening the primary circuit, *i.e.*, the moment of stimulation. Time-marker = Deprez's signal in the circuit of the tuning fork (*Burdon-Sanderson*).

powerful contraction, and when the weight attached to the muscle is small].

If the stimulus be applied to the motor nerve instead of to the muscle itself, the contraction is greater (*Pflüger*), and lasts longer (*Wundt*) the nearer to the spinal cord the stimulus is applied to the nerve.

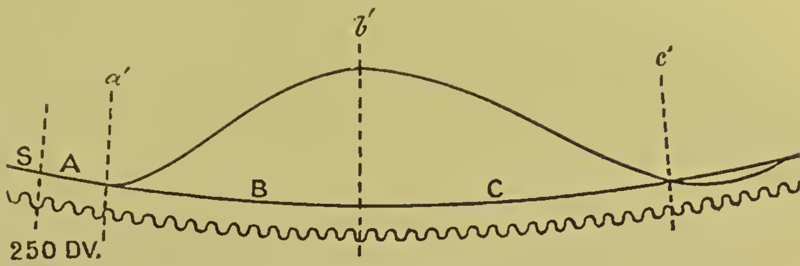


Fig. 396.

Pendulum myograph curve of a frog's gastrocnemius. S, point of stimulation; A, latent period; B, period of shortening, and C, of relaxation. 250 DV., tuning-fork vibrating 250 double vibrations per sec.] [The dotted vertical lines are ordinates (*Stirling*).

[In **studying a muscle-curve**, the more or less vertical character of the ascent will indicate the rapidity of the contraction, the height above the base line, its extent, the length of the curve, the duration, and the line of descent, the rate of its extensibility. The **form** of the muscle-curve will vary with the kind of myograph used; if it be stationary, then the muscle will merely record a vertical line; if the recording surface move quickly, the two parts of the curve will form an acute angle (fig. 398); and if it move with great rapidity, they will have the form of fig. 396, that obtained with a **pendulum myograph.** A vibrating tuning-fork records time directly under the tracing, whereby the duration of each part of the curve is readily determined.]

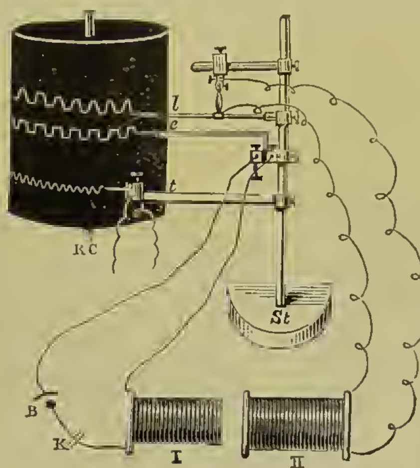


Fig. 397.

Arrangement for estimating the time-relations during contraction of a muscle produced by a faradic shock. B, battery; K, key in primary circuit; I, primary, II, secondary spiral; *l*, muscle lever; *c*, electro-magnet in primary circuit; *t*, electric signal; *St*, support; RC, revolving cylinder (after *Rutherford*).

[In **measuring the myogram**, all that is required is to know the moment at which the stimulus was applied, and to note when the curve begins to leave the base line or abscissa. Raise a vertical line or ordinate from each of these points, and the interval between these lines, as measured by the chronograph, indicates the time (fig. 396).]

[The **time-relations** of a simple muscular contraction caused by a **single induction shock** may be studied by means of the following arrangement:—Attach a frog's gastrocnemius to a lever, as in fig. 397, and through the frog's muscle place two wires from the secondary coil of an induction machine. A scale-pan with a weight is attached to the lever. On the same support adjust an electro-magnet with a writing-style in the primary circuit, and in this circuit also place a key (K) to make and break the current. Fix also a Dupré's chronograph to the same support, and make it vibrate by connecting it in circuit with a tuning-fork of known rate of vibration, and driven by a galvanic battery. See that the points of all three levers write exactly over each other on the revolving cylinder. The upper lever registers the contraction, the electro-magnet

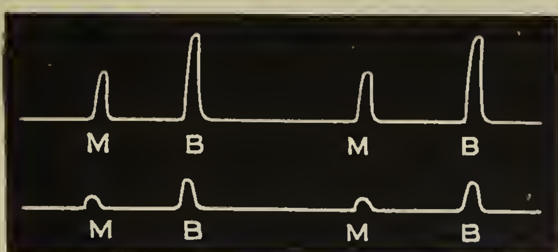


Fig. 398.

Frog's muscle stimulated alternately by a single break (B) and make shock (M). The lower curve shows the same, but with the muscle fatigued.

the moment the stimulus is applied to the muscle, and the electrical chronograph the time.]

[**Single make** (closing) or **break** (opening) **induction shocks.** A muscle or nerve may be stimulated either with a "make" or "break" induction shock, but it is important to notice that the break shock is stronger than the make. In fig. 398, B shows the effect produced by a single break induction shock, and M that of a single make shock.]

Overweighted Muscles.—The foregoing remarks apply to curves obtained by a *light* lever connected with the muscle. If the muscle lever be "*overweighted*," or **overloaded**, *i.e.*, if the lever be loaded, so that when the muscle contracts it has to lift these weights, the course of the curve varies according to the weight to be lifted. It is necessary, however, to support the lever in the intervals when the muscle is at rest. As the weights are increased, the occurrence of the contraction is delayed. This is due to the fact that the muscle, at the moment of stimulation, must accumulate as much energy as is necessary to lift the weight. The greater the weight, the longer is the time before it is raised. Lastly, the muscle may be so "loaded," or "overloaded," that it cannot contract at all; this is the limit of the muscular or mechanical energy of the muscle (*v. Helmholtz*).

Fatigue of Muscle.—If a muscle be caused to contract so frequently that it becomes "*fatigued*," the latent period is longer, the curve is not so high, because the muscular contraction is less, and the abscissa is longer, *i.e.*, the contraction is *slower* and lasts longer (fig. 399). *Cooling* a muscle has the same effect. Soltmann finds that the fresh muscles of *new-born* animals behave in a similar manner. The myogram has a flat apex and considerable elongation in the descending limb of the curve.

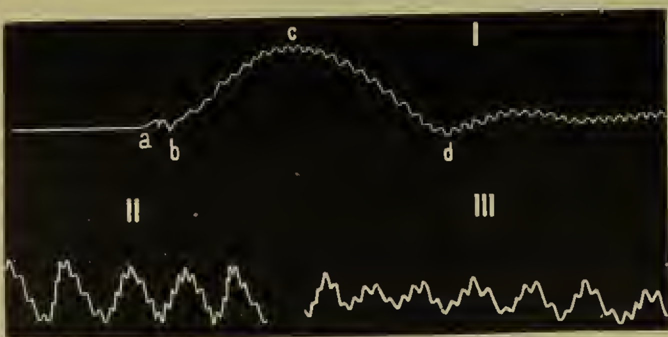


Fig. 399.

I, Contraction of a *fatigued* frog's muscle writing its contraction on a vibrating plate attached to a tuning-fork. Each vibration = 0·01613 second; *a b*, = latent period; *b c*, stage of increasing energy; *c d*, of decreasing energy. II. The most rapid writing movements of the right hand inscribed on a vibrating plate. III. The most rapid trembling tetanic movements of the right fore-arm inscribed on the same plate.

Constant Current. — If the **motor nerve** of a muscle be stimulated by a make or break shock of a *constant current*, the resulting muscular contraction corresponds exactly to that already described. If, however, the current be made or broken with the muscle itself directly in the circuit, during the make shock, *i.e.*, when the **muscle** is stimulated **directly** (the action of the nerves can be eliminated by using curare (§ 336)) there is a certain degree of contraction which lasts for a time, so that the curve assumes the form of fig. 400, where S represents the moment of closing or making the current, and Ö the moment of opening or breaking it (§ 336, D).

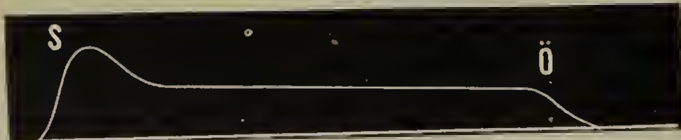


Fig. 400.

Effect on a muscle of closing and opening a constant current. S, closing; Ö, opening shock.

Variations in Muscles.—The investigations of Cash and Kronecker show that individual muscles have a special form of muscle-curve; the omohyoid of the tortoise contracts more rapidly than the pectoralis. Similar differences occur in the muscles of frogs and mammals. The flexors of the frog contract more rapidly than the extensors (*Grützner*). Sometimes within one and the same muscle there are "red" (rich in glycogen) and "pale" fibres (§ 292). The muscles of the tortoise, the adductor muscles of the mussel, and the heart contract slowly. The

red fibres contract more slowly, are less excitable, and less easily fatigued (*Grützner*). The muscles of flying insects contract very rapidly, even more than 360 times (fly) and 400 times (bee) per second.

The **pale muscles** are more excitable, have a longer latent period, are more readily fatigued, and their contraction is of shorter duration than the **red**. The pale muscles also produce more acid than the red muscles when they contract (*Gleiss*). The red muscles execute the prolonged continued movements, while the white execute more rapid movements. Muscles which are composed chiefly of pale fibres have a greater "lift" and a considerably greater absolute force during a single contraction, but during tetanus they are second to the red (*Grützner*). The muscle-curve of a muscle containing red and white fibres may show two elevations on the ascent, the first due to the rapidly contracting white fibres, and the second to the more slowly contracting red fibres. This also occurs after the action of strychnia on the muscle-substance (*Overend*).

Poisons.—Very small doses of **curare** or quinine increase the height of the contraction (excited by stimulation of the motor nerve), while larger doses diminish it, and finally abolish it altogether. **Guanidin** has a similar action in large doses, but the maximum of contraction lasts for a longer time. Suitable doses of **veratrin** also increase the contractions, but the stage of relaxation is greatly strengthened (*Rossbach and Clostermeyer*). **Veratrin**, antiarin, and digitalin, in *large* doses, act upon the sarcous substance in such a way that the contractions become very prolonged, not unlike a condition of prolonged tetanus (*Harless*, 1862). The latent period of muscles poisoned with veratrin and strychnin is shortened at first, and afterwards lengthened. The gastrocnemius of a frog supplied by blood containing soda contracts more rapidly (*Grützner*). Kunkel is of opinion that muscular poisons act by controlling the imbibition of water by the sarcous substances. As muscular contraction depends on imbibition (§ 297, II.), the form of the contraction of the poisoned muscle will depend upon the altered condition of imbibition produced by the drug.

[**Action of Veratrin.**—If a frog be poisoned with veratrin, and then be made to spring, it does so rapidly, but when it alights again the hind legs are extended, and they are only drawn up after a time. Thus, rapid and powerful contraction, with slow and prolonged relaxation, are the characters of the movement. In a muscle poisoned with veratrin, the ascent is quick enough, but it remains contracted for a long time, so that this condition has been called "**contracture.**" A single stimulation may cause a contraction lasting five to fifteen seconds, according to circumstances (fig. 401). Brunton and Cash find that cold has a marked effect on the action of veratrin—in fact, its effect may be permanently destroyed by exposure to extremes of heat or cold. The muscle-curve of a brainless frog cooled artificially, and then poisoned by veratrin, occasionally gives no indications of the action of the poison until its temperature is raised, and this is not due to non-absorption of the poison. Cold, therefore, abolishes or lessens the contracture peculiar to a veratrin-curve. Similar results are obtained with salts of **barium**, and to a less degree by those of strontium and calcium (*Brunton and Cash*).]

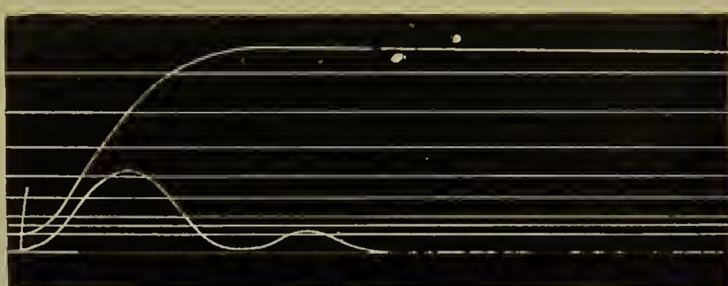


Fig. 401.
Lower curve is the normal muscle-curve (frog); upper one of the same muscle with veratrin (*Stirling*).

Smooth Muscles.—The muscle-curve of smooth or non-striped muscles is similar to that of the striped muscles, but the duration of the contraction is visibly much longer, and there are other points of difference. Some muscles stand midway between these two, at least as far as the duration of their contractions is concerned.

The "red" muscles of rabbits, the muscles of the tortoise, the adductors of the common mussel, and the heart, all react in a similar manner.

Contraction-Remainder.—A contracted muscle assumes its original length only when it is extended by sufficient traction, *e.g.*, by means of a weight. Otherwise,

the muscle may remain partially shortened for a long time. This condition has been called "**contracture**" (*Tiegel*), or, better, **contraction-remainder** (*Hermann*). This condition is most marked in muscles that have been previously subjected to strong, direct stimulation, and are greatly fatigued, which are distinctly acid, and ready to pass into rigor mortis, or in muscles excised from animals poisoned with veratrin (fig. 401).

"Contracture" also occurs in man. Mosso by means of his ergograph (§ 304) found that occasionally it was so marked that the muscles so affected sustained a weight of 3 kilos. It occurs at the beginning of a series of contractions and diminishes with increasing fatigue. It is least marked when executing voluntary contractions, and most marked during strong direct or indirect muscular contraction, Mosso regards it as a kind of fatigue, produced by too strong stimulation, manifested by a muscle at the beginning of its activity (*Mosso*).

Rapidity of Muscular Contraction.—In **man**, single muscular movements can be executed with great rapidity. The time-relations of such movements can be ascertained by inscribing the movements upon a smoked glass plate attached to a tuning-fork. Fig. 399, II, represents the most rapid *voluntary* movements that Landois could execute, as, *e.g.*, in writing the letters *n*, *n*, and every contraction is equal to about 3·5 vibrations (1 vibration = 0·01613 second) = 0·0564 second. In III, the right arm was tetanised, in which case 2 to 2·5 vibrations occur = 0·0323 to 0·0403 second.

V. Kries found that a simple muscular twitch, caused by a single induction shock, is shorter than a momentary voluntary single movement. If the thickening caused by a single voluntary contraction of a muscle be registered directly, the curve shows that the contraction within the muscle lasts longer than the duration of the movement produced in the passive motor apparatus itself. This paradoxical phenomenon is due to the fact that, shortly after the primary voluntary muscular contraction, there is a contraction of the antagonistic muscles, whereby a part of the intended movement is, as it were, cut off. During the most rapid voluntary movement in human muscles, v. Kries found that 4 stimuli per second were active, so that a voluntary contraction is really a short tetanus.

Pathological.—In secondary degeneration of the spinal cord after apoplexy, atrophic muscular anchylosis of the limbs, muscular atrophy, progressive ataxia, and paralysis agitans of long standing, the latent period is *lengthened;* while it is *shortened* in the contracture of senile chorea and spastic tabes (*Mendelssohn*). The whole curve is lengthened in jaundice and diabetes (*Edinger*). In cerebral hemiplegia, during the stage of contracture, the muscle-curve resembles the curve of a muscle poisoned with veratrin, and the same is the case in spastic spinal paralysis and amyotrophic lateral sclerosis; in pseudo-hypertrophy of the muscles the ascent is short and the descent very elongated. In muscular atrophy, after cerebral hemiplegia, and in tabes, the latent period increases, while the height of the curve diminishes. In chorea, the curve is short (*Reaction of Degeneration*, § 339). In rare cases in man, it has been observed that the execution of spontaneous movements results in a very prolonged contraction (**Thomsen's disease**). In such cases the muscular fibres are very broad, and the nuclei increased (*Erb*).

II. Action of Two Successive Stimuli.—Let two momentary stimuli be applied successively to a muscle:—**(A)** If *each stimulus* or shock be of itself sufficient to cause a "**maximal contraction**," *i.e.*, the greatest possible contraction which the muscle can accomplish, then the effect will vary according to the *time* which elapses between the application of the two stimuli. (*a*) If the second stimulus is applied to the muscle *after* the relaxation of the muscle following upon the first stimulus, we obtain merely two maximal contractions. (*b*) If, however, the second stimulus be applied to the muscle *during* the time that the effect of the first is present, *i.e.*, while the muscle is in the phase of contraction or of relaxation; in this case the second stimulus causes a new maximal contraction, according to the time of the particular phase of the contraction. (*c*) When, lastly, the second stimulus follows the first so rapidly that both occur during the latent period, we

obtain only *one* maximal contraction (*v. Helmholtz*). It is to be specially noted that a single maximal stimulus never excites the same degree of shortening as tetanic stimulation (III), but only about $\frac{1}{3}$ of the height of the contraction in tetanus.

(B) If the stimuli be not maximal, but only such as cause a medium or **sub-maximal** contraction, the effects of both stimuli are superposed, or there is a **summation** of the contractions (fig. 402). It is of no consequence at what particular phase of the primary contraction the second shock is applied. In all cases, the second stimulus causes a contraction, just as if the phase of contraction caused by the first shock was the natural passive form of the muscle, *i.e.*, the new contraction (b, c) starts from that point as from an abscissa (fig. 402, I, b). Thus, under favourable conditions, the contraction may be twice as great as that caused by the first stimulus. The most favourable time for the application of the second stimulus is $\frac{1}{20}$th second after the application of the first (*Sewall*). The effects of both stimuli are obtained even when the second stimulus is applied during the latent period (*v. Helmholtz*).

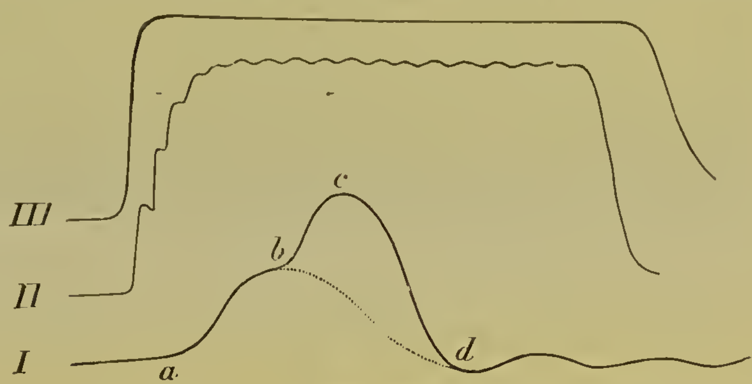


Fig. 402.

I, two successive sub-maximal contractions; II, successive contractions produced by stimulating a muscle with 12 induction shocks per second; III, curve produced with very rapid induction shocks (complete tetanus).

The second contraction of a summated contraction reaches its height in a shorter time than the first one would have done (*v. Frey, v. Kries*), *i.e.*, in fig. 402 the time for $b\ c$ is shorter than for $a\ b$.

III. Tetanus—Summation of Stimuli.—If stimuli, each capable of causing a contraction, and following each other with medium rapidity, be applied to a muscle, the muscle has not sufficient time to elongate or relax in the intervals of stimulation. Therefore, according to the rapidity of the successive stimuli, it remains in a condition of continued vibratory contraction, or in a state of **tetanus**. Tetanus is, however, not a continuous uniform condition of contraction, but it is a discontinuous condition or form of the muscle, depending upon the **summation** or accumulation of contractions. If the stimuli are applied with moderate rapidity, the individual contractions appear in the curve (fig. 402, II); if they occur rapidly, and thus become superposed and fused, the curve appears continuous and unbroken by elevations and depressions (fig. 402, III). As a fatigued muscle contracts slowly, it is evident that such a muscle will become tetanic by a smaller number of stimuli per second than will suffice for a fresh muscle (*Marey*). All muscular movements of *long duration* occurring in our bodies are probably tetanic in their nature (*Ed. Weber*).

The **number of stimuli** requisite to **produce tetanus** varies in different animals, and in different muscles of the same animal. About 15 stimuli per second are required to produce tetanus in the muscles of the **frog** (hyoglossus only 10, gastrocnemius 27, fig. 403); very feeble stimuli (more than 20 per second) cause tetanus (*Kronecker*); the muscles of the **tortoise** become tetanic with 2 to 3 shocks per second; the **red muscles** of the **rabbit** by 10, the **pale** by over 20 (*Kronecker and Stirling*); muscles of **birds** not even with 70 (*Marey*); muscles of **insects** 330 to 340 per second (*Marey*). Tetanic stimulation of the muscles of the crayfish

(Astacus) and also in Hydrophilus, may cause **rhythmical** contractions (*Richet*), or rhythmically interrupted tetanus (*Schönbein*).

[The number of stimuli required to produce tetanus in a frog's gastrocnemius is

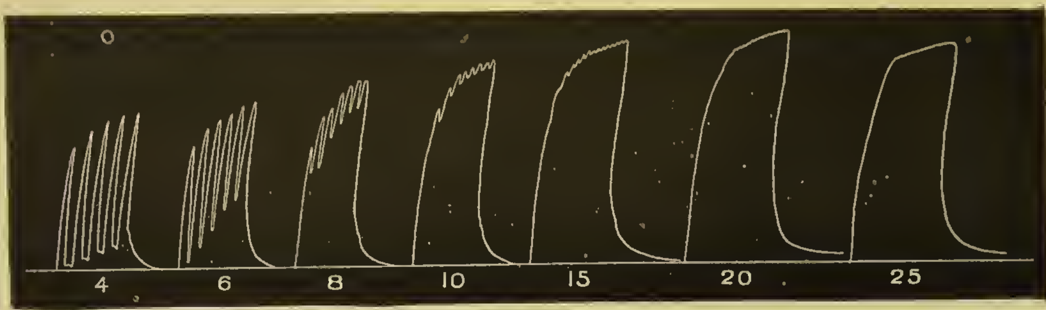


Fig. 403.

Curves showing the analysis of tetanus of a frog's muscle (gastrocnemius); the numbers under the curve indicate the number of shocks per second applied to the muscle. There is almost complete tetanus with 25 per sec. and it is a little lower than the previous one, because the muscle was slightly fatigued (*Stirling*).

shown in fig. 403, and also various stages of incomplete tetanus by applications of 4, 6, 8, 10, 15, 20, 25 stimuli per second, the last showing almost complete tetanus.]

[**Summation of Stimuli.**—If a stimulus, insufficient in itself to cause contraction of a muscle, be repeatedly applied to a muscle in proper tempo and of sufficient strength, at first a slight and then a stronger or maximal contraction may be produced. This process of summation occurs also in nervous tissue (§ 360).]

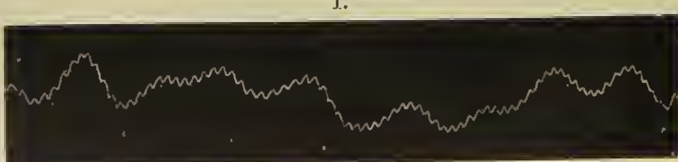
Minimal. Maximal. Sub-maximal. Maximal.

Fig. 404.

Four groups of contractions; interval of stimulation 2 seconds, and 5 minutes' pause between two groups.

[**Staircase** or **"Treppe."**—Bowditch showed that the cardiac contractions exhibited a "staircase" character, *i.e.*, the height of the second beat is greater than that of the first; and the third than that of the second (p. 94). The same occurs in the case of the muscles of the frog (*Tiegel, Minot*) and in mammals (*Rossbach*). Böhr showed that the successive ascending apices in a tetanus-curve have really a staircase character, and that its exact form is that of a hyperbola. Böhr found that (1) this form—the muscle not being fatigued—is independent of the strength and frequency of the stimuli. (2) The height of the series of contractions in tetanus is independent of the frequency of the stimuli, increase of frequency merely causing the staircase to reach its maximum more rapidly. (3) The height of the staircase increases—within certain limits—with the strength of the stimulus. Buckmaster has confirmed this for simple contractions, but as shown in fig. 404, when the stimuli are minimal or sub-maximal, there is usually no staircase character of the contractions, but maximal stimuli always cause it.]

I.



II.

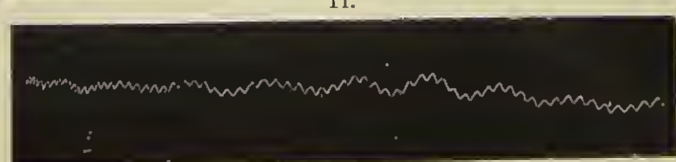


Fig. 405.

I., Vibration obtained from flexor brevis pollicis; II., from the extensor digiti tertii.

A continued **voluntary contraction** in man consists of a series of single contractions rapidly following each other. Every such movement, on being carefully analysed, consists of intermittent vibrations, which reach their maximum when a person shivers (*Ed. Weber*).—[Baxt found that the simplest possible voluntary contractions, *e.g.*, striking with the index finger, occupies on an average nearly twice as long a time as a similar movement discharged by a single induction-shock.]

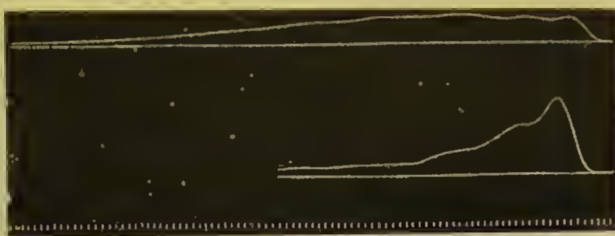


Fig. 406.

Curves obtained from red (upper) and pale (lower) muscles of a rabbit, by stimulating the sciatic nerve with a single induction shock. The lowest line indicates time, and is divided into $\frac{1}{100}$ second (*Kronecker and Stirling*).

The **number** of **single impulses** sent to our muscles during a voluntary movement is tolerably variable, during a slow contraction = 8 to 12, and during a rapid contraction = 18 to 20 impulses per second. Fig. 405, I., represents a myogram of a sustained contraction of the flexor brevis pollicis and abductor pollicis, recorded on a vibrating plate. The wave-like elevations indicate the single impulses, each tooth = 0·01613 second. II. is a similar curve registered by the extensor digiti tertii (*Landois*). [Schäfer finds that a prolonged voluntary contraction in man is an incomplete tetanus produced by 8 to 13 successive nervous impulses per second. About 10 per second may be taken as the average.]

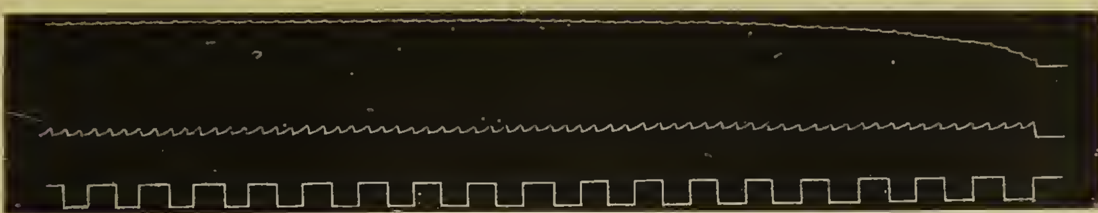


Fig. 407.

Make and break induction shocks of 300 units, applied at intervals of a $\frac{1}{4}$ second to the pale (lower) and red (upper) muscles of a rabbit. The lowest line marks $\frac{1}{4}$ second (*Kronecker and Stirling*).

Duration of Tetanus.—A tetanised muscle cannot remain contracted to the same extent for an indefinite period, even if the stimuli are kept constant. It gradually begins to elongate, at first somewhat rapidly, and then more slowly, owing to the occurrence of fatigue. If the tetanic stimulation is arrested, the muscle does not regain its original position and shape at once, but a contraction-remainder exists for a certain time, this being more evident after stimulation with induction shocks.

[**IV. If very rapid induction shocks** (224 to 360 per second) be applied to a muscle, the tetanus after a so-called "**initial contraction**" (*Bernstein*) may cease (*Harless*, *Heidenhain*). This occurs most readily when the nerves are cooled. Kronecker and Stirling, however, found that stimuli following each other at greater rapidity than 24,000 per second produced tetanus.

[**Tone-inductorium of Kronecker and Stirling.**—This apparatus (fig. 408), consists of a rod of iron, *d*, fixed in an iron upright at *a*. The primary, $s_{,}$, and secondary spiral, $s_{,,}$, rest on wooden supports, which can be pushed over both ends of the rod. One end of the rod lies between leather rollers, *f* and *g*, which can be made to rub on the rod by moving the toothed wheels, *h*. In this way a tone is produced by the **longitudinal vibrations** of the rod, the number of vibrations being proportional to the length of the rod, so that by means of this instrument we can produce from 1000 to 24,000 alternating induction shocks per second.]

Isometrical Muscular Acts.—Fick has recently investigated the changes—

tension—undergone by a muscle when it is stimulated, and when its length remains constant, and he calls this process an "**isometrical muscular act.**" He finds that a voluntary contraction in an isometrical act in man causes a higher

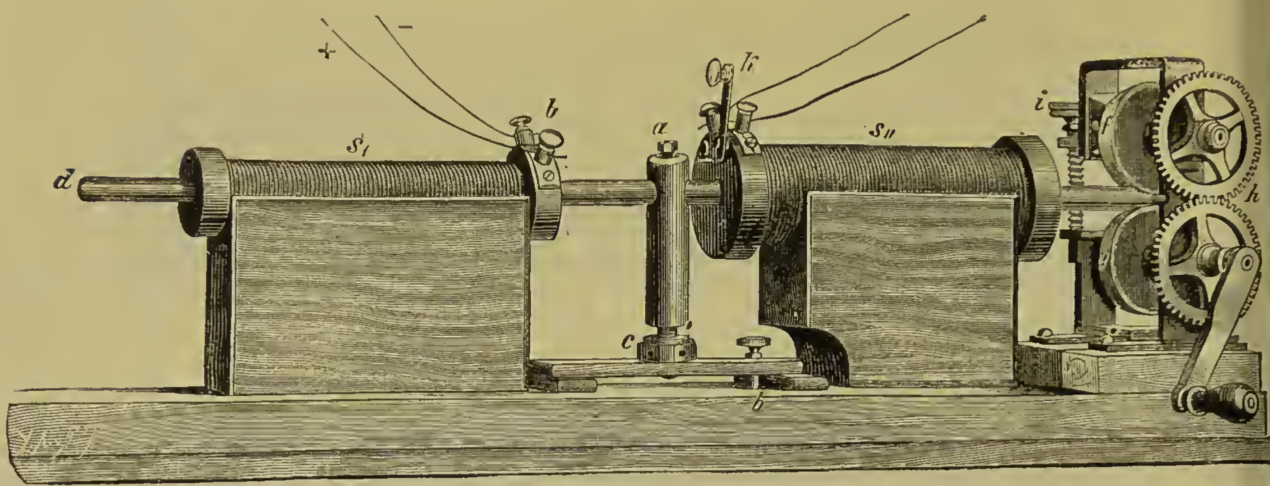


Fig. 408.

Tone-inductorium of Kronecker and Stirling. *d*, iron rod, clamped at *a*; $s_{,}$ primary, $s_{,,}$ secondary spiral, with a key, *k*; leather rollers, *f* and *g*, driven by wheels, *h*.

tension than a contraction excited electrically. In the frog, the tension is nearly twice as great during tetanus as during a single maximal muscular contraction; in human muscles, it may be ten times as great.

299.—RAPIDITY OF TRANSMISSION OF A CONTRACTION.—1. If a long muscle be stimulated **at one end**, a contraction occurs at that point, and is rapidly propagated in a **wave-like** manner through the whole length of the muscle, until it reaches its other end. The condition of excitement or molecular disturbance is communicated to each successive part of the muscle, in virtue of a special conductive capacity of the muscle. The mean **velocity of the contraction-wave** is 3 to 4 metres per second in the frog (*Bernstein*, 3·869 metres); rabbit, 4 to 5 metres (*Bernstein and Steiner*); lobster, 1 metre (*Fredericq*); in **smooth muscle** and in the **heart**, only 10 to 15 millimetres per second (§ 58, 4). These results have reference only to excised muscles, the velocity of transmission being much greater in the voluntary muscles of a living man, viz., 10 to 13 metres (*Hermann*, § 334, II.).

Methods.—(1) Aeby placed writing-levers upon both ends of a muscle, the levers resting transversely to the direction of the muscular fibres. The muscle was stimulated, and both levers registered their movements, the one directly over the other on a revolving cylinder. On stimulating one end of the muscle, the lever nearest to this point is raised by the contraction-wave, and a little later the other lever. When we know the rate at which the cylinder is moving and the distance between the two elevations, it is easy to calculate the rapidity of transmission of the contraction-wave.

[(2) Marey measured the rate of propagation of the wave of contraction by his "**pinces myographiques**" (fig. 409, 1, 2) each of which is connected to a recording tambour (1′, 2′).

When one end of the muscle is stimulated, *e.g.*, at 1 the thickening which occurs during contraction of a muscle affects the first tambour, and as the wave of contraction passes along the muscle it affects the second tambour, so that two tracings are obtained on the drum. The two curves do not coincide, for that traced by 2′ occurs slightly later than that traced by 1′, the interval of time representing the time which the wave of contraction took to travel from 1 to 2.]

Duration and Wave-Length.—The time, corresponding to the length of the abscissa of the muscle-curve inscribed by each writing-lever, is equal to the *dura-*

tion of the contraction of this part of the muscle (according to Bernstein, 0·053 to 0·098 second). If this value be multiplied by the rapidity of transmission of the muscular contraction-wave, we obtain the *wave-length* of the *contraction-wave* (= 206 to 380 millimetres).

Modifying Influences.—Cold (fig. 410), fatigue, approaching death, and many

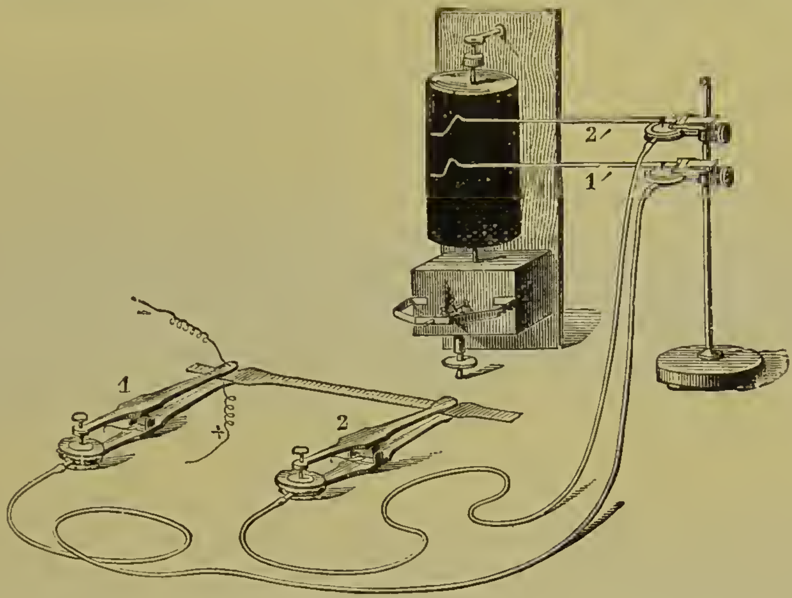


Fig. 409.
Pinces myographiques of Marey (1 and 2); 1′ and 2′ recording tambours.

poisons [veratrin, KCy] diminish the velocity and the height of the contraction-wave, while the strength of the stimulus and the extent to which the muscle is loaded are without any effect upon the velocity of the wave (*Aeby*). In excised muscles, the size of the wave diminishes as it passes along the muscle, but this is not the case in the muscles of living men and animals. The contraction - wave never passes from one muscular fibre to a neighbouring fibre.

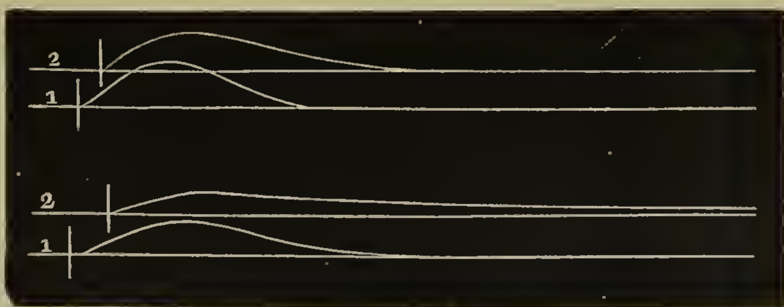


Fig. 410.
Upper two curves, 2 and 1, obtained from a rabbit's muscle by the above arrangement; the lower two curves from the same muscle when it was cooled by ice.

[Fig. 410 shows the effect of cold on the muscles of a rabbit, in delaying the contraction-wave. There is a longer distance between 1 and 2 in the lower than in the upper curves.]

2. If a long muscle be stimulated locally **near its middle**, a contraction-wave is propagated towards both ends of the muscle. If several points be stimulated simultaneously, a wave movement sets out from each, the waves passing over each other in their course (*Schiff*).

3. If a stimulus be applied to the **motor nerve** of a muscle, an impulse is specially communicated to *every muscular fibre ;* a contraction-wave begins at the *end-organ* [motorial end-plate], and must be propagated in both directions along

the muscular fibres, whose length is only 5–9 centimetres. As the length of the motor fibres from the nerve-trunk to where they terminate in the motorial end-plates is unequal, contraction of all the muscular fibres cannot take place absolutely at the same moment, as the nerve-impulse takes a certain time to travel along a nerve. Nevertheless, the difference is so small that, when a muscle is caused to contract by stimulation of its motor nerve, practically the whole muscle appears to contract simultaneously and at once.

4. *A complete, uniform, momentary contraction of all the fibres* of a muscle can only take place when all the fibres are excited at the same moment. This occurs when the electrodes are placed at both ends of the muscle, and an electrical stimulus of momentary duration passes through the whole length of the muscle.

300. MUSCULAR WORK.—Muscles are most perfect machines, not only because they make the most thorough use of the substances on which their activity depends (§ 217), but they are distinguished from all machines of human manufacture by the fact that by frequent exercise they become stronger, and are thereby capable of accomplishing more work (*Du Bois-Reymond*).

The **amount of mechanical work** (W) which a muscle can perform is equal to the product of the weight lifted (p) and the height to which it is lifted (h), *i.e.*, $W = ph$ (*Introduction*), or

$$\text{height} \times \text{weight} = \text{work}.$$

Hence it follows that when a muscle is not loaded (where $p = 0$), then w must be $= 0$, *i.e.*, no work is performed. If, again, it be overloaded with too great a load, so that it is unable to contract ($h = 0$), here also the work is nil. Between these two extremes an active muscle is capable of doing a certain amount of "mechanical work."

I. **Work with Maximal Stimulation.**—When the strongest possible, or **maximal stimulus** is applied—*i.e.*, when the strength of the stimulus is such as to cause a muscle to contract to the greatest possible extent of which it is capable, the amount of work done increases more and more as the weight is increased, but only up to a certain maximum. If the weight be gradually increased, so that it is lifted to a less height, the amount of work diminishes more and more, and gradually falls to be $= 0$, when the weight is not lifted at all.

Example of the work done by a frog's muscle (*Ed. Weber*):—

Weight lifted in Grams.	Height in Millimetres.	Work done in Gram-Millimetres.
5	27·6	138
15	25·1	376
25	11·45	286
30	7·3	220

[Suppose a muscle be loaded with a certain number of grams, and then caused to contract, we get a certain height of contraction. Fig. 411 shows the result of an experiment of this kind. The vertical lines represent the height to which the weights (in grams) noted under them were raised, so that, as a rule, as the weight increases the height to which it is raised decreases.]

Laws of Muscular Work.—1. A muscle can lift a greater load the larger its transverse section, *i.e.*, the more fibres it contains arranged parallel to each other.

2. The longer the muscle, the higher it can lift a weight.

3. When a muscle begins to contract, it can lift the largest load; as the contraction proceeds, it can only lift a less and less load, and when it is at its maximum of shortening, only relatively very light loads.

4. By the term "**absolute muscular force**" is meant, according to Ed. Weber, just the weight which a muscle undergoing maximal stimulation is no longer able to lift (the muscle being in its normal resting phase), and without the muscle at the moment of stimulation being elongated by the weight.

Comparative.—Comparing the **absolute muscular force** of different muscles, even in different animals, it is usual to calculate it with reference to that of a square centimetre. The mean transverse section of a muscle is obtained by dividing its volume by its length. The volume is equal to the absolute weight of the muscles divided by its specific gravity = 1058. The absolute muscular force for 1 □ centimetre of a frog's muscle = 2·8 to 3 kilos. [6·6 lbs.] (*J. Rosenthal*); for 1 □ centimetre of human muscle = 7 to 8 (*Henke and Knorz*), or even 9 to 10 kilos. [20 to 23 lbs.] (*Korster, Haughton*). **Insects** can perform an extraordinary amount of work—an insect can drag along sixty-seven times its body-weight; a horse scarcely three times its own weight.

5. During **tetanus**, when a weight is kept suspended, no work is done as long as the weight is suspended, but of course work is done in the act of lifting the load. To produce tetanus, successive stimuli are required, the muscular metabolism is increased, and fatigue rapidly occurs. The potential energy in this case is converted into heat (§ 302). When a muscle is stimulated with a *maximal stimulus*, it cannot lift so great a weight with *one* contraction as when it is stimulated tetanically (*Hermann*). The energy evolved, even during tetanus, is greater the more frequent the stimulation, at least up to 100 stimuli per second (*Bernstein*).

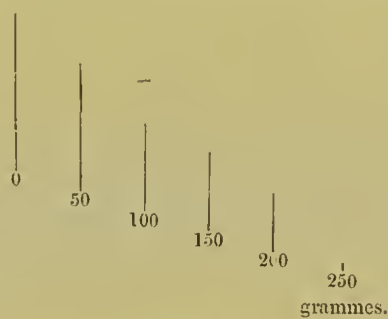


Fig. 411.
Height to which each of the weights is raised.

II. Medium Stimuli.—If a muscle be caused to contract by stimuli of *moderate strength*, *i.e.*, such as do not cause a maximal contraction, there are two possibilities: Either the feeble stimulus is kept constant whilst the load is varied, in which case the amount of work done follows the same law as obtains for maximal stimulation; or, the load may be kept the same, whilst the strength of the stimulus is varied. In the latter case Fick observed that the height to which the load was lifted increased in a direct ratio with the strength of the stimulus.

The stimulus which causes a muscle to contract must reach a certain strength or intensity before it becomes effective, *i.e.*, the "**liminal intensity**" of the stimulus, but this is independent of the weight applied to the muscle. With minimal stimuli, a small weight is raised higher than a large one, but as the stimulus is increased, the contractions also increase in a larger ratio with an increased load (*v. Kries*).

The **blood-stream** within the muscles of an intact body is increased during muscular activity. The **blood-vessels** of the muscle **dilate**, so that the amount of blood flowing through them is increased (*Ludwig and Sczelkow*). At the time that the motor fibres are excited, so also are the **vaso-dilator fibres**, which lie in the same nervous channels (§ 294, II.). [Gaskell found that faradisation of the nerve of the mylohyoid muscle of the frog not only caused tetanus of the muscle, but also dilatation of its blood-vessels.]

Testing Individual Muscles.—In estimating the **absolute force** of the *individual muscles* or groups of muscles in man, we must always pay particular attention to the physical relations, *i.e.*, to the arrangement of the levers, direction of the traction, degree of shortening, &c. (§ 306). **Dynamometer.**—The absolute force of certain groups of muscles is very conveniently and practically ascertained by means of a dynamometer (fig. 412). This instrument is very useful for testing the difference between the power of the two arms in cases of paralysis. The patient grasps the instrument in his hand and an index registers the force exerted. Quetelet has estimated the force of certain muscles—the pressure of both hands of a man to be = 70 kilos.; while by pulling he can move double this weight. The force of the female hand is one-third less. A man can carry more than double his own weight; a woman about the half of this. Boys can carry about one-third more than girls. [Very convenient dynamometers are made by Salter of Birmingham, both for testing the strength of **pull** and **squeeze**; in testing the former, the instrument is held as an archer holds his bow when in the act of drawing it, and the strength of pull is given by an index; in the latter another form of the instrument is used. Large numbers of observations were made by means of these instruments by Francis Galton at the Health Exhibition, 1885.]

Amount of Work Daily.—In estimating the work done by a man, we have to consider, not only the amount of work done at any one moment, but how often, time after time, he can succeed in doing work. The mean value of the daily work of a man working eight hours a day is 10 (10·5 to 11 at most) kilogram-metres per second, *i.e.*, a daily amount of work = 288,000 (300,000) kilogram-metres.

[**Ergostat.**—Sometimes it is desirable that patients—especially those who suffer from excessive corpulence—should do a certain amount of work daily; this can be carried out by Gaertner's Ergostat, which resembles a winch, driven by a handle. The pressure upon the wheel can be regulated by means of a strap, lever, and weights, and according to the weight and number of revolutions of the wheel, can the amount of mechanical work be accurately regulated. This instrument is recommended for therapeutical purposes.]

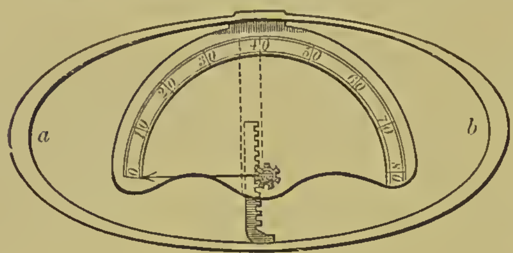


Fig. 412.
Dynamometer of Mathieu.

Modifying Conditions.—Many substances, after being introduced into the body, **diminish**, and ultimately paralyse the production of work—mercury, digitalin, helleborin, potash salts, &c. Others **increase** the muscular activity—veratrin (*Rossbach*), glycogen, [caffein, and allied alkaloids], muscarin, (*Klug and Fr. Högyes*), kreatin and hypoxanthin; extract of meat rapidly restores the muscles after fatigue (*Kobert*). [Those drugs which excite muscular tissue restore it after fatigue. Kreatin is a waste product of muscle, and beef-tea and Liebig's extract of meat perhaps owe their restorative qualities partly to these extractives.]

301. **THE ELASTICITY OF MUSCLE.**—**Physical.**—Every elastic body has its "natural shape," *i.e.*, its shape when no external force (tension or pressure) acts upon it so as to distort it. Thus, the passive muscle has a "natural form." If, however, a muscle be extended in the course of its fibres, the parts of the muscle are evidently pulled asunder. If the stretching be carried only to a certain degree, the muscle, in virtue of its elasticity, will regain its natural form. Such a body is said to possess "**complete elasticity**," *i.e.*, after being stretched it regains exactly its original shape. By the term "**amount of elasticity**" (*modulus*) is meant the weight (expressed in kilograms) necessary to extend an elastic body 1 □ millimetre in diameter, its own length, without the body breaking. Of course many bodies are ruptured before this occurs. For a passive muscle it is = 0·2734 (*Wundt*) [that of bone = 2264 (*Wertheim*), tendon = 1·6693, nerve = 1·0905, the arterial walls = 0·0726 (*Wundt*).] Thus, the amount of elasticity of a passive muscle is small, as it requires only a slight stretching force to extend it to its own length. It has, therefore, no great amount of elasticity. The term "**coefficient of elasticity**" is applied to the fraction of the length of an elastic body, to which it is elongated by the unit of weight applied to stretch it. It is large in a passive muscle. If the tension be sufficiently great, the elastic body ruptures at last. The "*carrying capacity*" of muscular tissue, until it ruptures, is in the following ratios for youth, middle, and old age, nearly 7 : 3 : 2. [Instead of the word "elasticity," Brunton suggests the use of **extensibility** and **retractibility**, terms suggested by Marey, the one referable to the elongation on the application of a weight, and the other to the shortening after its removal.]

Curve of Elasticity.—In **inorganic elastic bodies** the line of elongation, or

Fig. 413.

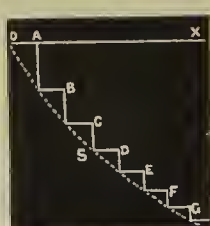


Fig. 414.

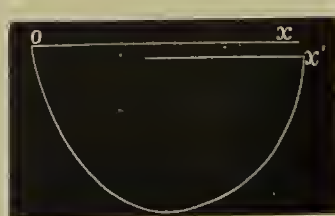


Fig. 415.

Fig. 413.—Curve of elasticity from an inorganic body (india-rubber). Fig. 414.—Curve of elasticity from the sartorius of a frog, obtained by adding equal increments of weight at A, B, C, &c. Fig. 415.—Curve of elasticity produced by continuous extension and recoil of a frog's muscle; *o x*, abscissa before, *x'* after extension.

the *extension, is directly proportional to the extending weight* (Hooke's law) in inorganic bodies, and therefore in muscle this is not the case, as the weight is continually increased by equal increments—the muscle is less extended than at

the beginning, so that the extension is *not proportional to the weight.* If equal weights be added to a scale-pan attached to a piece of india-rubber, with a writing-lever connected with it, and writing its movements on a plate of glass that can be moved with the hand, we get such a curve as in fig. 413, while, if the same be done with the sartorius of a frog, we get a result similar to fig. 414. A **straight line** joins the apices of the former, while the curve of elasticity is a **hyperbola**, or something near it, in the latter case.

Elastic After-Effect.—At the same time, after the first elongation, corresponding to the extending weight, is reached, the muscle may remain for days, and even weeks, somewhat elongated. This is called the "*elastic after-effect*" (§ 65). [Marey attached a lever to a frog's muscle, and allowed the latter to record its movements on a slowly revolving cylinder. To the lever was fixed a vessel into which mercury slowly flowed. This extended the muscle, and when it had ceased to elongate, the mercury was allowed slowly to run out again. The curve obtained is shown in fig. 415. The abscissæ, $o\ x$ and x', indicate the position of the writing style before and after the experiment, and we observe that x' is lower than $o\ x$, so that the recoil is imperfect. There has been an actual elongation of the muscle, so that the limit of its elasticity is exceeded. Although a frog's gastrocnemius may be loaded with 1500 grams without rupturing it, 100 grams will prevent its regaining its original length.]

Method.—In order to test the **elasticity** of a muscle, fix it to a support provided with a graduated scale, and to the lower end of the muscle attach a scale-pan, in which are placed various weights, measuring on each occasion the corresponding elongation of the muscle thereby obtained (*Ed. Weber*). In order to obtain the **curve of elongation** or **extensibility**, take as abscissæ the successive units of weight added, and the elongation corresponding to each weight as ordinates. Example from the hyoglossus of the frog:—

Weight in Grams.	Length of the Muscle in Millimetres.	Extension.	
		In Millimetres.	Percentage.
0·3	24·9	...	...
1·3	30·0	5·1	20
2·3	32·3	2·3	7
3·3	33·4	1·1	3
4·3	34·2	0·8	2
5·3	34·6	0·4	1

The elasticity of passive muscle is **small** in amount, but **very complete**, and is comparable to that of caoutchouc. Small weights greatly elongate a muscle. If the weights be uniformly increased, there is not a uniform elongation; with equal increments of weight, the greater the load, the increase in elongation always becomes less; or, to express it in another way, the amount of elasticity of the passive muscle increases with its increased extension (*Ed. Weber*).

In **inorganic bodies** the **curve of extension** is a **straight line**, but in **organic** bodies it more closely resembles a **hyperbola** (*Wertheim*). The elasticity of a passive *fatigued* muscle does not differ essentially from that of a non-fatigued muscle.

Fresh Muscles.—Muscles in the living body, and still in connection with their nerves and blood-vessels, are more extensible than excised ones. Muscles, when quite fresh, are elongated (within certain small limits as regards the weight) at first with a uniformly increasing weight, to an extent proportional to the latter, just as with an inorganic body. When heavy weights are used, we must be careful to take into consideration the "*elastic after-effect*" (§ 65).

The volume of a stretched muscle is slightly *less* than an unstretched one, similar to the contracted (§ 297, 2) and stiffened muscle (§ 295).

Dead muscles and muscles in **rigor mortis** have a greater amount of elasticity, *i.e.*, they

require a heavier weight to stretch them than fresh muscles; but, on the other hand, the elasticity of dead muscles is less complete, *i.e.*, after they are stretched, they only recover their original form within certain limits.

Elasticity of Intact Muscles.—Normally, within the body, the muscles are stretched to a very slight extent, as can be shown by the slight degree of retraction which occurs when the insertion of a muscle is divided. This slight degree of extension, or stretching, is important. If this were not so, when a muscle is about to contract and before it could act upon a bone as a lever, it would have to "take in so much slack." The elasticity of muscles is manifested during the contraction of antagonistic muscles. The position of a passive limb depends upon the resultant of the elastic tension of the different muscle groups.

The elasticity of an active muscle is less than that of a passive muscle, *i.e.*, it is elongated by the same weight to a greater extent than a passive muscle. For this reason the active muscle, as can be shown in an excised contracted muscle, is *softer;* the apparently great hardness manifested by stretched contracted muscles depends upon their tension. When the active muscle becomes **fatigued**, its elasticity is diminished. [This is readily seen in a fatigue-curve, where the muscle lever no longer reaches the abscissa] (§ 304).

Method.—Ed. Weber took the hyoglossus muscle of a frog and suspended it vertically, noticing its length when it was passive. It was then tetanised with induction shocks and its height again noted. One after the other heavier weights were attached to it, and the length of the passive and tetanised muscle observed for each weight. The extent to which the active loaded muscle shortened from the position of the passive loaded muscle he called the "height of the lift" (or "Hubhöhe"). The latter becomes less as the weight increases, and lastly, the tetanised muscle may be so loaded that it cannot contract, *i.e.*, the height of the lift is = 0.

Weber's Paradox.—The case may occur where, when a muscle is so loaded that it cannot contract when it is stimulated, it may even **elongate**. According to Wundt, even in this condition the elasticity is not changed. [The usual explanation given is that, as the elasticity of a muscle is diminished during contraction, it is more extended with the same weight in the contracted as compared with the passive or uncontracted state, so that a heavily weighted muscle, when stimulated, may elongate instead of shorten.] According to Wundt, however, as stated, there is no change in the elasticity of the muscle. In these experiments, the length of the active loaded muscle is equal to the length of the passive muscle when similarly loaded, minus the "height of the lift."

Drugs.—Potash causes shortening of a muscle with simultaneous increase of its elasticity. Digitalin produces other changes with increased elasticity. Physostigmin increases it, while veratrin diminishes it, and interferes with its completeness (*Rossbach and v. Anrep*), and tannin makes a muscle less extensible, but more elastic (*Lewin*). Ligature of the blood-vessels produces at first a decrease, and then an increase, of the elasticity; section of the motor nerve diminishes the elasticity (*v. Anrep*); heat increases it.

Eduard Weber concluded from his experiments that a muscle assumes two forms, the active and the passive form. Each of these corresponds to a special natural form. The passive muscle is longer and thinner—the active is shorter and thicker in form. The passive as well as the active muscle strives to retain its form. If the passive muscle be set into activity, the passive rapidly changes into the active form, in virtue of its elastic force. The latter is the energy which causes muscular work. Schwann compared the force of an active muscle to a long, elastic, tense spiral spring. Both can lift the greatest weight, only from that form in which they are most stretched. The more they shorten, the less the weight which they can lift.

[**Uses of Elasticity.**—As already pointed out, all muscles are slightly on the stretch, so that no time is lost nor energy wasted, in "taking in slack," as it were; but the elasticity also lessens the shock of the contraction, so that it is developed gradually, and muscles are not liable to be torn from their attachments. The muscular energy is transmitted to the mass to be moved through an elastic and easily extensible body (muscle), whereby the shock due to the contraction is lessened, but, as Marey has shown, the amount of work is thereby considerably increased.]

[**Tonicity of Muscle** (§ 362)—**Sensibility of Muscle.**—That muscles contain sensory fibres is certain (§ 430). Section of inflamed muscles is painful, and during muscular cramp intense pain is felt. Sachs discharged a reflex action by stimulating the central end of an intra-muscular

nerve-filament in a frog, while stimulation of the central end of the phrenic nerve raises the blood-pressure (*Muscular Sense*, § 430).]

302. Formation of Heat in an Active Muscle.—After Bunzen, in 1805 (§ 210, 1, *b*), showed that during muscular activity heat is evolved, v. Helmholtz proved that an *excised* frog's muscle, when *tetanised* for two to three minutes, exhibited an **increase of its temperature** of 0·14° to 0·18° C. R. Heidenhain succeeded in showing an increase of 0·001° to 0·005° C. for each *single contraction*. The same is true of the beating heart which is warmer during every systole (*Marey*). There is a very short latent period before the rise of temperature.

[**Method.**—The rise in temperature of a frog's muscle may be estimated by placing the two gastrocnemii muscles of a frog on the two junctions of a thermo-electric pile, connected with a heat galvanometer. Of course, when the two muscles are at the same temperature, the needle of the galvanometer is stationary; but, if one muscle is made to contract, or is tetanised, then an electrical current is set up which deflects the needle (§ 208 B). Lujankow has, by means of a delicate thermometer placed between the thigh muscles of a dog, estimated the rise of temperature under different conditions of the muscle, while the latter was still *in situ* and intact.]

The following facts have been ascertained with regard to the development of heat:—

1. **Relation to Mechanical Work.**—It bears a relation to the amount of work.

(a) If a muscle during contraction carries a weight which extends it again during rest, no work is transferred beyond the muscle (§ 300). In this case all the chemical potential energy during this movement is converted into heat. Under these circumstances, the amount of heat evolved runs parallel with the amount of work done, *i.e.*, it increases as the load and the height increase up to a maximum point, and afterwards diminishes as the load is increased. The heat-maximum is reached with a less load sooner than the work-maximum (*Heidenhain*).

(b) If, when the muscle is at the height of its contraction, the *load be removed*, then the muscle has produced work referable to something outside itself; in this case the amount of heat produced is less (*A. Fick*). The amount of work produced, and the diminished amount of heat formed, when taken together, represent the same amount of energy, corresponding to the law of the conservation of energy.

(c) If the same amount of work is performed in one case by many but small contractions, and in another by fewer but larger contractions, then in the latter case the amount of heat is greater (*Heidenhain and Nawalichin*). This shows that larger contractions are accompanied by a *relatively* greater metabolism of the muscular substance than small contractions, which is in harmony with practical experience; thus the ascent of a tower with steep high steps causes fatigue more rapidly (metabolism greater) than the ascent of a more gentle slope with lower steps.

(d) If the weighted muscle executes a series of contractions one after the other, and at the same time does work, then the amount of heat it produces is greater than when it is tetanic, and keeps a weight suspended. Thus, the transition of the muscle into a shortened form causes a greater production of heat than the maintenance of this form.

2. **Relation to Tension.**—The amount of heat evolved depends upon the *tension of the muscle;* it also increases as the muscular tension increases (*Heidenhain*). If the ends of a muscle be so fixed that it cannot contract, the maximum of heat is obtained (*Béclard*), and this the more quickly the more rapidly the stimuli follow each other (*Fick*). Such a condition occurs during tetanus, in which condition the violently contracted muscles oppose each other, and very high temperatures have been registered by Wunderlich (§ 213, 7), while the same is true of animals that are tetanised (*Leyden*). Dogs kept in a state of tetanus by electrical stimulation die, because their temperature rises so high (44° to 45° C.) that life can no longer be maintained (*Richet*). In addition to the

formation of heat, there is a considerable amount of *acid*, and of alcoholic extractives produced in the muscular tissue.

3. **Relation to Stretching.**—Heat is also evolved during the *elongation* or relaxation of a contracted muscle, *e.g.*, by causing a muscle to contract without the addition of any weight, and loading it when it begins to relax, whereby heat is produced (*Steiner, Schmulewitsch, and Westerman*). If weights be attached to a muscle by means of an inextensible medium, and the weights be allowed to fall from a height so as to give a jerk to the muscle, then an amount of heat equivalent to the work done by the drop is set free in the muscle (*Fick and Danilewsky*).

4. **Fatigue.** — The formation of heat diminishes as the muscular fatigue increases, and as the muscle recovers it increases (*Fick*).

5. **Blood Supply.**—In a muscle duly supplied with blood the production of heat (as well as the mechanical work) is far more active than in a muscle whose blood-vessels are ligatured or the blood-stream of which is cut off. Recovery takes place more rapidly and completely after fatigue, while, at the same time, there is a new increase in the production of heat (*Meade Smith*).

The amount of work and heat in a muscle must always correspond to the transformation of an equivalent amount of chemical energy. A greater part of this energy is manifested as work, the greater the resistance that is offered to the muscular contraction. When the resistance is great, ¼ of the chemical energy may be manifested as work, but when it is small, only a small part of it is so converted.

When the temperature is increased, as in **fever**, there is a greater metabolism in the muscle with the production of more heat, but without increasing the amount of work done.

In man, if the muscles be stimulated with electricity or contracted voluntarily, the production of heat may be detected through the skin (*v. Ziemssen*). The venous blood flowing from an actively contracting muscle is 0·6° C. warmer than the arterial blood (*Meade Smith*).

It was stated that a **nerve** in action is $\frac{1}{50}$° C. warmer (*Valentin*), but this is denied by v. Helmholtz and Heidenhain; a dying nerve, however, becomes warmer (*Rollcston*).

303. **THE MUSCLE-SOUND.—Resting and active Muscle.**—When a muscle contracts, and is at the same time kept in a state of tension by the application of sufficient resistance, it emits a distinct sound or **tone** with a semi-musical quality, depending upon the intermittent variations of tension occurring within it (*Wollaston*).

Methods.—The muscle-sound may be heard by placing the ear over the tetanically contracted and tense biceps of another person; or we may insert the tips of our index fingers into our ears, and forcibly contract the muscles of our arm; or the sound of the muscles that close the jaw may be heard by forcibly contracting them, especially at night when all is still, and when the outer ears are closed. V. Helmholtz found that this tone coincides with the resonance tone of the ear, and he thought that the vibrations of the muscles caused this resonance tone. The sound of an isolated frog's muscle may be heard by placing one end of a rod in the ear, the other ear being closed. To the other end of the rod is attached a loaded frog's muscle kept in a tetanic condition. The pitch of the note, *i.e.*, the number of vibrations, may be estimated by comparing the muscle-sound with that produced by elastic springs vibrating at a known rate.

When a muscle contracts **voluntarily**, *i.e.*, through the will, it makes 19·5 vibrations per second. [Schäfer and others give the number as 10 successive nervous impulses per second, p. 603.] We do not hear this very low tone, owing to the number of vibrations per second being too few, but what we actually hear is the *first overtone*, with double the number of vibrations. The muscle-sound has 19·5 vibrations, when the muscles of an animal are caused to contract, by stimulating its *spinal cord* (*v. Helmholtz*), and also when the *motor nerve-trunk* is excited by chemical means (*Bernstein*). If, however, **tetanising** induction shocks be applied to a muscle, then the number of vibrations of the muscle-sound corresponds exactly with the number of vibrations of the vibrating spring or hammer of the induction apparatus. Thus the tone may be raised or lowered by altering the tension of the spring.

Lovèn found that the muscle-sound was loudest when the weakest currents capable of producing tetanus were employed. The sound corresponded to the number of vibrations of the

octave just below it in the scale. With stronger currents the muscle sound disappears, but it reappears with the same number of vibrations as that of the interrupter of the induction apparatus, if still stronger currents are used.

If the induction shocks be applied to the **nerve** the sound is not so loud, but it has the same number of vibrations as the interrupter. With rapid induction shocks, tones caused by 704 (*Lovèn*) and 1000 vibrations per second have been produced (*Bernstein*).

A single induction shock is said to cause the muscle-sound in a contracting muscle. If this be so, it is doubtful if the muscle-sound can be regarded as a sign that tetanus is due to a series of single variations of the muscle (§ 298, III.).

[The **first heart-sound** is said to be partly muscular and partly valvular (§ 53), and, as already stated, Krehl has recently confirmed this view originally supported by Ludwig and Dogiel. Haycraft, however, states that the first sound is a valvular sound like the second sound.]

[Bernstein has shown that a muscle-sound may be produced during a single contraction of a muscle, which is not due to friction of the muscle on its surroundings. Stimulation of a muscle by a single induction shock causes a short sharp sound ("contraction sound.") It coincides with the period of "negative variation."]

[**Resting living muscle** *versus* **active muscle.**—It might be well to sum up the chief differences between a living resting or passive muscle and one actively contracting. When a muscle contracts it undergoes physical and chemical changes, resulting in the conversion of the energy of chemical affinity into other forms of energy.

1. The **naked eye changes** are that the muscle becomes shorter and thicker with scarcely any appreciable change in its volume, thus resulting in mechanical motion.

2. **Microscopic changes.**—It is admitted by all that the dim bands become broader across the fibre, and correspondingly thinner in the length of the fibre. Some say that the bright discs undergo similar changes. Under the polariscope both bands are seen to retain their specific characters in relation to the action of light.

3. **Thermal changes.**—Heat is given off by a resting muscle, but the heat evolved is increased during contraction.

4. **Changes of electrical potential.**—The contracted part becomes negative to the uncontracted part of the muscle, *i.e.*, there is a current of action, or, put in another way, the electrical response results in a diminution of the muscle-current or the so-called "negative variation."

5. **Other physical changes.**—The elasticity is diminished, the extensibility is increased, and the sound—the "muscle-sound"—is emitted.

6. The **chemical changes** in an active muscle are similar to those that occur in a muscle at rest, but on contraction taking place, there is a sudden increase of those changes. *Gases*—The contracting muscle gives off more CO_2, and takes up more O, but not in proportion to the CO_2 given off. *Reaction*—There is an increased formation of lactic acid, so that, with continued contraction, the muscle may become acid. *Extractives*—During tetanus, at least, the extractives soluble in water decrease, and those soluble in alcohol increase. Some reducing substances seem to be produced, but there is no evidence that the proteids of the muscle itself undergo a change.]

304. **FATIGUE AND RECOVERY OF MUSCLE.**—By the term **fatigue** is meant that condition of diminished capacity for work which is produced in a muscle by prolonged activity. This condition is accompanied in the living person with a peculiar feeling of lassitude, which is referred to the muscles. A fatigued muscle rapidly **recovers** in a living animal, but an excised muscle recovers only to a slight extent (*Ed. Weber*, *Valentin*).

[Waller recognises a certain resemblance between experimental fatigue and the natural decline of excitability at death, in disease, and in poisoning.]

The **cause of fatigue** is probably partly due to the accumulation of decomposition products—"**fatigue stuffs**"—in the muscular tissue, these products being formed within the muscle itself during its activity. They are *phosphoric acid*, either free or in the form of acid phosphates, *acid potassium phosphate* (§ 294), glycerin-phosphoric acid (?) and CO_2. If these substances be removed from a muscle, by passing through its blood-vessels an indifferent solution of common salt (0·6 per cent.), or a weak solution of sodium carbonate [or a dilute solution of permanganate of potash (*Kronecker*)], the muscle again becomes capable of energising (*J. Ranke*, 1863). The using up of O by an active muscle favours fatigue (*v. Pettenkofer and v. Voit*). The transfusion of *arterial blood* (not of venous—*Bichat*) removes the fatigue (*Ranke, Kronecker*), probably by replacing the substances that have been used up in the muscle. Conversely, an actively energising muscle may be rapidly fatigued by injecting into its blood-vessels a dilute solution of phosphoric acid, of acid potassium phosphate, or dissolved extract of meat (*Kemmerich*). A muscle fatigued in this way absorbs less O, and when so fatigued, it evolves only a small amount of acids and CO_2. The conditions which lead up to fatigue are connected with considerable metabolism in the muscular tissue.

[**Massage**—Zabludowski found that if a frog's muscles be systematically stimulated by maximum induction shocks until they cease to contract, **massage** or kneading them rapidly restored their excitability, while simple rest had little effect. Massage acts on the nerves, but chiefly by favouring the blood- and lymph-streams which wash out the waste products from the muscle. A similar result obtains in man, so that the ancient Roman practice of "rubbing" after a bath and after exercise was one conducive to restoration of the power of the muscles.]

Conditions modifying fatigue.—In order to obtain the same amount of work from a fatigued muscle, a much more powerful stimulus must be applied to it than to a fresh one. A fatigued muscle is incapable of lifting a considerable load, so that its absolute muscular force is diminished. If, during the course of an experiment, an excised muscle be loaded with the same weight, and if the muscle be stimulated at regular intervals with maximal stimuli (strong induction shocks), contraction after contraction gradually and regularly diminishes in height, the decrease being a constant fraction of the total shortening. Thus the fatigue-curve is represented by a *straight line* [*i.e.*, a straight line will touch the apices of all the contractions]. The more rapidly the contractions succeed each other, the greater is the fall in the height of the contraction [*i.e.*, if the *interval* between the contractions be short, the fatigue-curve falls rapidly towards the abscissa], and conversely. After a certain number of contractions an excised muscle becomes exhausted.

This result occurs whether the stimuli are applied at short or long intervals (*Kronecker*), and a similar result is obtained with sub-maximal stimuli (*Tiegel*). A fatigued muscle contracts more *slowly* than a fresh one, while the latent period is also longer during fatigue (p. 595). The fatigued muscle is said to be more extensible (*Donders and van Mansvelt*). If a muscle be so loaded that, when it contracts, it cannot lift the load, fatigue occurs even to a greater extent than when the load is such that the muscle can lift it (*Leber*). The metabolism and the formation of acid are greater in a contracted muscle kept on the stretch than in a contracted muscle allowed to shorten (*Heidenhain*). If a muscle contract, but be not required to lift any load, it becomes fatigued only very gradually. If a muscle be loaded only during contraction, and not during relaxation, it is fatigued more slowly than when it is loaded during both phases; and the same is true when a muscle has to lift its load only during the *course* of its contraction, instead of at the beginning of the contraction. A load may be suspended to a perfectly passive muscle without fatiguing it (*Harless, Leber*).

[**Signs of fatigue** (fig. 416).—In the record of the series of contractions; (1)

the contractions become more prolonged; (2) they decrease in height; (3) the latent period becomes longer; (4) if maximal shocks be used, the beginning of the series exhibits a "staircase" character of its contractions, just like the heart (§ 57).]

[While an excised frog's muscle is fairly rapidly exhausted by single opening induction shocks, at intervals of one second, human muscle in its normal relations may be almost indefinitely so treated, and there is no change in the record or any sensation of fatigue. Waller regards this as favouring the view that the "fatigue consequent upon prolonged muscular exertion is normally central rather than peripheral." Such results, however, do not harmonise with those of Zabludowski on the kneading of muscles, or massage. Probably there are two factors, one central, the other peripheral.]

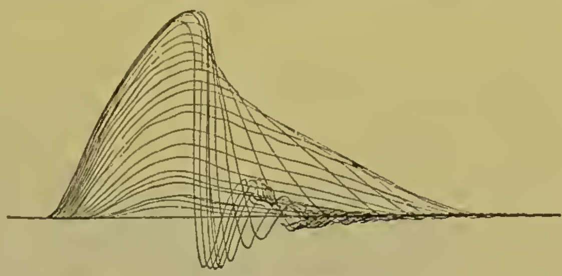


Fig. 416.

Fatigue-curve of a frog's muscle. The sciatic nerve was stimulated with maximal induction shocks and every fifteenth contraction recorded (*Stirling*).

Blood Supply.—If the arteries of a mammal be ligatured, stimulation of the motor nerves produces complete fatigue after 120 to 240 contractions (in two to four minutes), but direct muscular stimulation still causes the muscles to contract. In both cases the fatigue-curve is in the form of a straight line. If the blood supply to a mammalian muscle be normal, on stimulating the motor nerve, the muscular contractions at first increase in height and then fall, their apices forming a straight line (*Rossbach and Harteneck*). In persons who have used their muscles until fatigue sets in, it is found that at the beginning the nerves and muscles react better to galvanic and faradic stimulation, but afterwards always to a less degree (*Orschanski*). According to v. Kries, a muscle tetanised and fatigued with maximal stimuli behaves like a fresh muscle tetanised with sub-maximal stimuli; both show an incomplete transition from the passive to the active condition.

[**Relation of End-Plates.**—Muscle is fatigued far more rapidly than nerve, and the fatigue begins in the muscle and not in the nerve; it seems to be the weakest link in the chain between nerve and muscle which is affected during excessive action, viz., the motor **end-plate** (*Waller*). In a **nerve** its conductivity is sooner affected by fatigue than its direct excitability. Waller finds that after death "the excitability of a nerve persists when its action upon muscle has ceased, such muscle being still excitable by direct stimulation." Some link in the chain is obviously affected, and it is perhaps the end-plates.]

[**Relation of Drugs to Fatigue.**—Waller finds, in a frog poisoned with veratrin, that if the muscles be stimulated electrically, the characteristic elongation of the descent (§ 298) gradually disappears, but reappears after a period of rest. In this respect, strychnin in its action on the spinal cord behaves precisely the same as veratrin on muscle, viz., its effect is dissipated by action and restored by rest.] Curare and the ptomaines cause an irregular course of the fatigue-curve (*Guareschi and Mosso*). [If strychnin be injected into a frog, and the sciatic nerve on one side divided after the strychnin tetanus has lasted for a time, the leg muscles of the side with the nerve undivided exhibit signs of fatigue, as shown by direct stimulation of the muscles of both legs, when a curve similar to fig. 417 is obtained. The higher one is the non-fatigued, the lower that of the side with the nerve undivided (*Waller*).]

Fig. 417.

Curves obtained by direct stimulation of the gastrocnemius of a frog poisoned with strychnin, the sciatic nerve divided on one side (upper curve) and not on the other (lower or fatigue-curve).

Recovery from the condition of fatigue is promoted by passing a *constant electrical current* through the entire length of the muscle (*Heidenhain*), also by injecting fresh arterial blood into its blood-vessel, or by very small doses of veratrin, [or permanganate of potash], and by rest.

If the muscle of an intact animal be stimulated continuously (fourteen days or so), until complete fatigue occurs, the muscular fibres become granular and exhibit a wax-like degeneration. The transverse striation is still visible as long as the sarcous substance is in large masses, but as soon as it breaks up into small pieces the transverse striation disappears completely (*O. Roth*).

[**Fatigue experiments on man with the Ergograph.**—Mosso and Maggiora

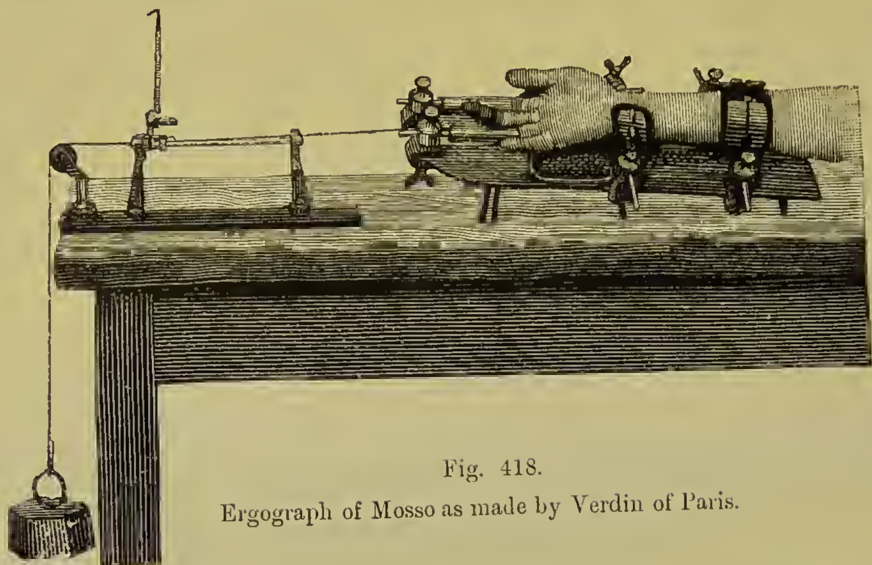


Fig. 418.
Ergograph of Mosso as made by Verdin of Paris.

fixed the fore-arm in an appropriate holder and attached the middle finger to a string to which a weight was added. The person experimented on contracted his flexor muscles and thus raised at a given signal a given weight, the extent of the movement being recorded simultaneously. This in principle is the **ergograph** shown in fig. 418.]

Muscles excited to contract directly become sooner fatigued than those excited

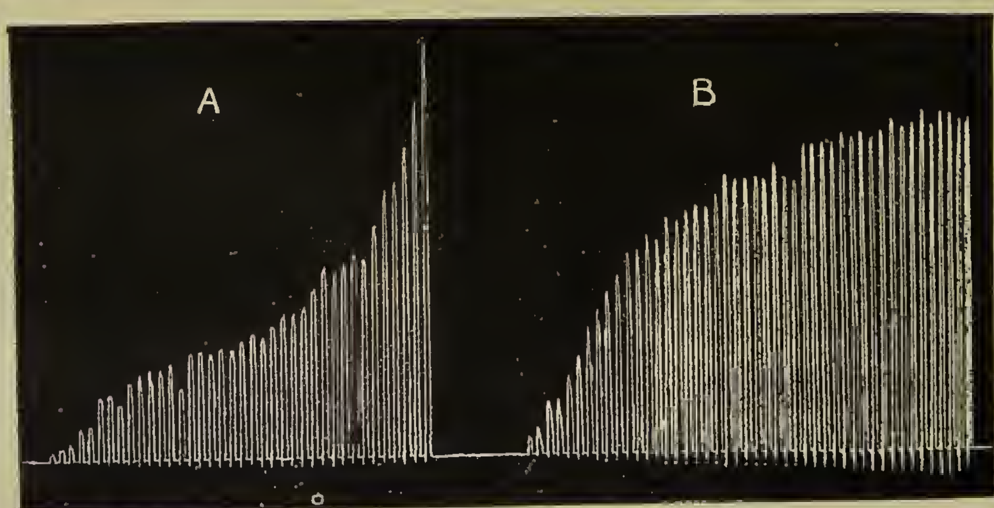


Fig. 419.
Curves obtained by the ergograph from two individuals, A and B.

indirectly (*i.e.*, through their nerve). The fatigue-curve is a straight line only for medium weights, for small weights it is S-shaped, and for larger ones it is a hyperbola.

[Kronecker found in the case of frog's muscle stimulated electrically, that the "fatigue-curve" was a straight line gradually falling towards the abscissa (p. 614). Mosso, however, finds that more usually the curve obtained is like fig. 419, A, or fig. 419, B, and that the form of curve is nearly constant for each individual under the same conditions; and, as a matter of fact, he has shown that the fatigue-curve obtained by raising a weight of 3 kilos. with the ergograph remains constant over an interval of several years.]

A muscle tetanised continuously by electrical stimuli until its muscular energy is apparently exhausted, still retains some energy, which can be called into action by the will. Conversely, a muscle which no longer contracts in obedience to volitional stimuli will contract when stimulated by electrical stimuli. If electrical and volitional stimuli act directly the one after the other, in this way complete exhaustion and fatigue of the muscle may be brought about. Mental work diminishes considerably the muscular force. The most powerful volitional muscular contractions cannot be increased by strong electrical stimulation of the motor nerves. On the contrary, if the motor nerve is strongly stimulated, so as to cause a slightly stronger contraction, then the will cannot cause the muscle to contract still more. Anæmia causes symptoms similar to fatigue, but a free supply of blood rapidly restores the muscle. Fatigue of the legs, as in walking, accelerates the fatigue of the arms. Sustained wakefulness and fasting facilitate fatigue. Massage favours the disappearance of fatigue (*Maggiora*). [There would seem to be a central nervous factor associated with the production of muscular fatigue; for if a muscle be made to contract voluntarily until it no longer responds to volitional stimuli, and if meantime it be stimulated to contract by means of electrical stimuli, it again—although it has been contracting—becomes capable of responding to volitional stimuli. It would seem as if the nerve-centres also became fatigued during muscular fatigue. They had apparently recovered in the interval. Work done by a fatigued muscle produces far more injurious consequences than a far larger amount done by the muscle under normal conditions. Fatigue of other muscles than in those to be investigated, *e.g.*, forced marching, fatigues even the unused muscles, *e.g.*, of the arms.]

305. STRUCTURE AND MECHANISM OF BONES AND JOINTS.—Bones exhibit in the inner architecture of their spongiosa an arrangement of their lamellæ and spicules which represents the static result of those forces—pressure and traction—which act on the developing bone (§ 447). They are so arranged that, with the minimum of material, they afford the greatest resistance as a supporting structure or framework (*H. v. Meyer*, *Culmann*, *Jul. Wolff*).

[**Structure of Bone.**—Next to enamel, bone is the hardest tissue in the body. Its hardness is due to the presence of lime-salts, chiefly phosphate of lime. If a bone be steeped for some time in dilute hydrochloric acid, the lime-salts are extracted and the bone loses its rigidity; it becomes soft, and pliable, and can be cut with a knife; indeed, such a bone, *e.g.*, rib or fibula, may be tied into a knot. The bone, when softened or decalcified, still retains the shape and general structure of the original bone. If a bone be burned it first chars, and, finally, only the ash remains. The organic matter is all burned off, and now the bone is quite brittle.]

[The **chemical composition** of dry bone is approximately as follows:—

Ossein (collagen), or animal matter,	31·03	Calcic fluoride,	1·41
Calcic phosphate,	58·23	Magnesic phosphate,	1·32
Calcic carbonate,	7·32	Sodic chloride,	0·69]

[If a longitudinal section be made of a long dried bone, the outer part is seen to be **dense** or **compact**; while, more interiorly, more especially towards the extremities of the bone, the bony texture is more **cancellated** or **spongy**. There is, however, a gradual transition from dense to spongy bone. The spicules of bone which bound the cancelli or spaces in cancellated bone are arranged in a definite order in each bone, corresponding to the lines of pressure and stress. This constitutes the architecture of the bones. In the central part of every long bone is a cavity, the **medullary cavity**, which in the fresh condition contains the marrow.]

[Bone consists of **cells embedded in a fibrous matrix.**—The **cells** or **bone-corpuscles**, are branched corpuscles (fig. 422). The **matrix** consists of interlacing fibres, and there is a ground-substance which contains the lime salts. The cor-

puscles lie in spaces of the matrix called **lacunæ**, and adjoining lacunæ communicate by numerous fine canals—**canaliculi**—which perforate the matrix (fig. 420).]

[A fresh bone is really a **complex organ**. It is invested externally by a fibrous membrane, the **periosteum**, in which numerous arteries ramify before they enter the bone. The arteries pass into the bone through small apertures, ramify, and run in channels in the compact bone, the **Haversian canals** (fig. 421). The medullary canal contains marrow, and so do the cancelli at the ends of the bone. The medullary canal is lined by a thin vascular membrane, the **endosteum.**]

[**Microscopic Structure of Macerated Compact Bone.**—A thin transverse section of the shaft of such a bone is made up of **lamellæ**, or plates disposed as follows:—Some of them are arranged concentrically with reference to the outer surface of the bone, *i.e.*, immediately under the periosteum—these are the **peripheric lamellæ**; others (5–15) are arranged around the sections of the Haversian canals,—these are the **Haversian lamellæ**, and each Haversian canal with its lamellæ constitutes an **Haversian system** (fig. 420). Some vestiges of lamellæ lie between the Haversian systems, but they always are arcs of circles with longer radii than the Haversian lamellæ; they are **intermediate** or **interstitial lamellæ** (fig. 420, *sl*). Some lamellæ are arranged with reference to the central marrow cavity, and are the **peri-medullary lamellæ**.]

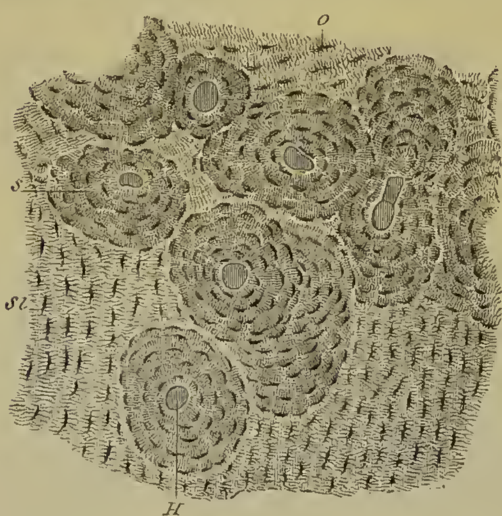


Fig. 420.

Transverse section of part of the shaft of a human femur. H, Haversian canals; *s*, Haversian lamellæ; *sl*, interstitial lamellæ; *o*, lacunæ with canaliculi. × 40.

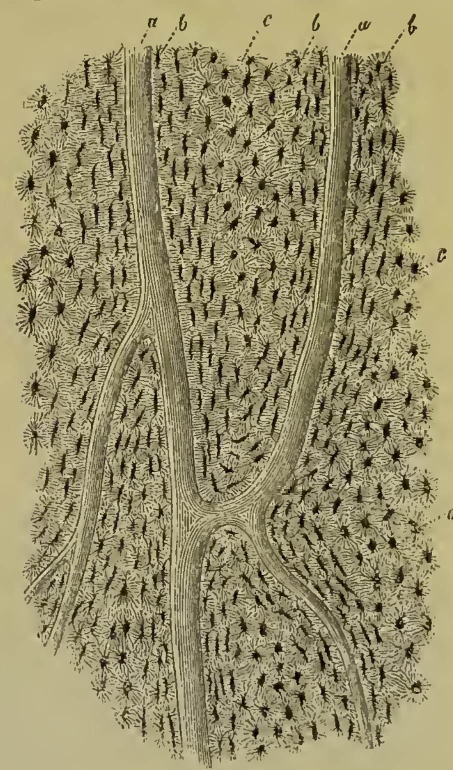


Fig. 421.

Longitudinal section of the diaphysis of a human femur × 100. *a*, Haversian canals; *b*, lacunæ seen from the side; *c*, from the surface.

[In the transverse section of each Haversian system are sections of oval flattened spaces, arranged concentrically—the **lacunæ** (fig. 420). They appear black, because in dry bone they are filled with air. From these lacunæ **canaliculi**, or fine branching tubes, proceed, and perforate the lamellæ, so that the canaliculi from adjacent lacunæ anastomose. The innermost lacunæ communicate with the Haversian canal of their own system, and by this canalicular system lymph is carried to the bone-corpuscles, which lie in the lacunæ and quite close to the outermost part of each Haversian system. The canaliculi from the outermost lacunæ of

any Haversian system do not communicate with the canaliculi of adjacent systems, but they bend on themselves, and open into the lacunæ of their own system, and hence they have been called **recurrent canaliculi.**]

[The arrangement of the lacunæ in the other parts of the bone follow the arrangement of the lamellæ, several lamellæ usually intervening between two adjacent rows of lacunæ.]

[**Sharpey's Fibres** are calcified fibres which pierce obliquely or at right angles the peripheric and interstitial lamellæ. Some of them are calcified white fibrous tissue, and others are yellow or elastic fibres. The latter are more abundant in the bones of birds.]

[The appearance presented by a longitudinal section of compact dry bone is shown in fig. 421.]

[The **periosteum** is a laminated fibrous membrane, composed chiefly of fibrous tissue. It consists of an **outer fibrous layer**, which contains many blood-vessels, and branches of the latter, accompanied by connective-tissue, pass into the Haversian canals. The **inner layer** contains some fibrous tissue, also many elastic fibres, and, especially in young bones, numerous nucleated, somewhat cubical, cells—the **osteoblasts**, or **bone-forming cells.** The osteoblasts form several layers in young bones, and in adult bones they exist as thin flattened cells, lying on the outermost peripheric lamellæ. They are carried into the interior of the bone, along the

Fig. 422.

Transverse section of a part of the shaft of a long bone, decalcified and stained with picrocarmine (*Stirling*). × 350.

Haversian canals, with the blood-vessels. They form bone—secrete or form bone around themselves—and, in doing so, become embedded, as it were, in the products of their own activity; and, when so embedded in osseous tissue, they are then called **bone-corpuscles**, so that bone-corpuscles are embedded osteoblasts. In a section of a softened fresh bone which has been stained, it is easy to see bone-corpuscles lying in their lacunæ (fig. 422).]

[The **marrow of bone** is of two varieties, yellow and red. **Yellow marrow** occurs in the medullary canal, and is for the most part made up of fat-cells. **Red marrow**, however, occurs chiefly in the heads of large bones, in short bones, ribs, flat bones of the skull, and is really a **blood-forming organ** (§ 7). It contains several varieties of cells—small, round, nucleated cells—the marrow cell closely

resembling lymph-corpuscles; others, not unlike these, but with a yellowish tint, the erythroblasts, from which red blood-corpuscles are formed. It also contains large multi-nucleated cells, **osteoclasts** or **myeloplaxes.** These osteoclasts absorb or eat away bone, and are the structures concerned in the absorption of bone during certain stages of bone-development (fig. 422).]

I. **The joints** permit the freest movements of one bone upon another [such as exist between the extremities of the bones of the limbs. In other cases sutures are formed, which, while permitting no movement, allow the contents of the cavity which they surround to enlarge, as in the case of the cranium]. The articular end of a fresh bone is covered with a thin layer or plate of **hyaline cartilage,** or **"encrusting cartilage,"** which in virtue of its elasticity moderates any shocks or impulses communicated to the bones. The surface of the articular cartilage is perfectly smooth, and facilitates an easy gliding movement of the one surface upon the other. At the outer boundary line of the cartilage there is fixed the **capsule** of the joint, which encloses the articular ends of the bones like a sac. The inner surface of the capsule is lined by a **synovial membrane,** which secretes the sticky, semi-fluid, **synovia,** moistening the joint. The outer surface of the capsule is provided at various parts with bands of fibrous tissue, some of which strengthen it, whilst others *restrain* or limit the movement of the joint. Some osseous processes limit the movements of particular joints, *e.g.*, the coronoid process of the ulna, which permits the fore-arm to be flexed on the upper arm only to a certain extent; the olecranon, which prevents over-extension at the elbow-joint. The joint-surfaces are kept in apposition—(1) by the adhesion of the synovia-covered smooth articular surface; (2) by the capsule and its fibrous bands: and (3) by the elastic tension and contraction of the muscles.

[**Structure of Articular Cartilage.**—The thin layer of hyaline encrusting cartilage is fixed by an irregular surface upon the corresponding surface of the head of the bone (fig. 423). In a vertical section through the articular cartilage of a bone which has been softened in chromic or other suitable acid, we observe that the cartilage-cells are flattened near the free surface of the cartilage, and their long axes are parallel to the surface of the joint; lower down, the cells are arranged in irregular groups, and further down still, nearer the bone, in columns or rows, whose long axis is in the long axis of the bone. These rows are produced by transverse cleavage of pre-existing cells. In the upper two-thirds or thereby the matrix of the cartilage is **hyaline,** but in the lower third, near the bone, the matrix is granular and sometimes fibrillated. This is the **calcified zone,** which is impregnated with lime salts, and sharply defined by a *nearly straight line* from the hyaline zone above it, and by a very bold *wavy line* from the osseous head of the bone.]

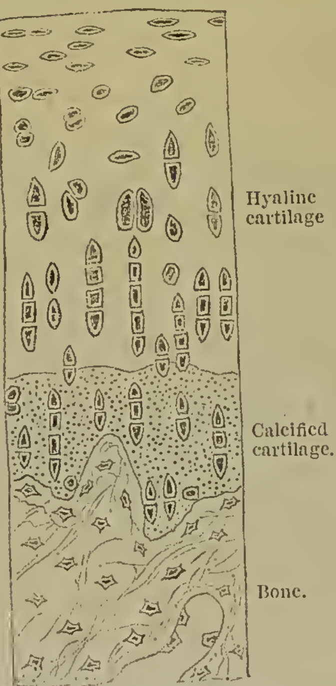


Fig. 423.
Vertical section of articular cartilage (*Stirling*).

Synovial Membrane. — Synovial membrane consists of bundles of delicate connective-tissue mixed with elastic tissue, while on its inner surface it is provided with folds, some of which contain fat, and others blood-vessels (synovial villi). The inner surface is lined with endothelium. The intra-capsular ligaments and cartilages are not covered by the synovial membrane, nor are they covered by endothelium.

The **synovia** is a colourless, stringy, alkaline fluid, with a chemical composition closely allied to that of transudations, with this difference, that it contains much **mucin,** together with albumin and traces of fat. Excessive movement diminishes its amount, makes it more inspissated, and increases the mucin, but diminishes the salts.

Joints may be divided into several classes, according to the kind of movement which they permit:—

1. **Joints with movement round one axis:** (*a*) **The Ginglymus,** or **Hinge-Joint.**—The one articular surface represents a portion of a cylinder or sphere, to which the other surface is adapted by a corresponding depression, so that, when flexion or extension of the joint takes

place, it moves only on *one* axis of the cylinder or sphere. The joints of the fingers and toes are hinge-joints of this description. *Lateral* ligaments, which prevent a lateral displacement of the articular surfaces, are always present.

The Screw-hinge Joint is a modification of the simple hinge form (*Langer*, *Henke*), *e.g.*, the humero-ulnar articulation. Strictly speaking, simple flexion and extension do not take place at the elbow-joint, but the ulna moves on the capitellum of the humerus like a nut on a bolt; in the right humerus, the screw is a right spiral, in the left, a left spiral. The ankle-joint is another example; the nut or female screw is the tibial surface, the right joint is like a left-handed screw, the left the reverse. (*b*) The **Pivot-Joint (rotatoria)**, with a cylindrical surface, *e.g.*, the joint between the atlas and the axis, the axis of rotation being around the odontoid process of the axis. In the acts of **pronation** and **supination** of the fore-arm at the elbow-joint, the axis of rotation is from the middle of the cotyloid cavity of the head of the radius to the styloid process of the ulna. The other joints which assist in these movements are *above* the joint, between the circumferential part of the head of the radius and the sigmoid cavity of the ulna, and *below* the joint, between the sigmoid cavity of the radius which moves over the rounded lower end of the ulna.

2. **Joints with movements round two axes.**—(*a*) Such joints have two unequally curved surfaces which intersect each other, but which lie in the same direction, *e.g.*, the atlanto-occipital joint, or the wrist-joint, at which lateral movements, as well as flexion and extension, take place. (*b*) Joints with curved surfaces, which intersect each other, but which do not lie in the same direction. To this group belong the **saddle-shaped** articulations, whose surface is concave in one direction, but convex in the other, *e.g.*, the joint between the metacarpal bone of the thumb and the trapezium. The chief movements are—(1) flexion and extension, (2) abduction and adduction. Further, to a limited degree, movement is possible in all other directions; and, lastly, a pyramidal movement can be described by the thumb.

3. **Joints with movement on a spiral articular surface (spiral joints)**, *e.g.*, the knee-joint (*Goodsir*). The condyle of the femur, curved from before backwards, in the antero-posterior section of its articular surface, represents a *spiral* (*Ed. Weber*), whose centre lies nearer the posterior part of the condyle, and whose radius vector increases from behind, downwards and forwards. Flexion and extension are the chief movements. The strong lateral ligaments arise from the condyles of the femur corresponding to the centre of the spiral, and are inserted into the head of the fibula and internal condyle of the tibia. When the knee-joint is strongly flexed, the lateral ligaments are relaxed—they become tense as the extension increases; and when the knee-joint is fully extended, they act quite like tense bands which secure the lateral fixation of the joint. Corresponding to the spiral form of the articular surface, flexion and extension do not take place around *one* axis, but the axis moves continually with the point of contact; the axis moves also in a spiral direction. The greatest flexion and extension cover an angle of about 145°. The anterior crucial ligament is more tense during extension, and acts as a check ligament for too great extension, while the posterior is more tense during flexion, and is a check ligament for too great flexion. The movements of extension and flexion at the knee are further complicated by the fact that the joint has a screw-like movement, in that during the greater extension the leg moves outwards. Hence, the thigh, when the leg is fixed, must be rotated outwards during flexion. Pronation and supination take place during the greatest flexion to the extent of 41° (*Albert*) at the knee-joint, while with the greatest extension it is nil. It occurs because the external condyle of the tibia rotates on the internal. In all positions during flexion, the crucial ligaments are fairly and uniformly tense, whereby the articular surfaces are against each other. Owing to their arrangement, during increasing tension of the anterior ligament (extension), the condyles of the femur must roll more on to the anterior part of the articular surface of the tibia, while by increasing tension of the posterior ligament (flexion), they must pass more backwards.

4. **Joints with the axis of rotation round one fixed point.**—These are the freely movable arthrodial joints. The movements can take place around innumerable axes, which all intersect each other in the centre of rotation. One articular surface is nearly spherical, the other is cup-shaped. The shoulder and hip-joints are typical "**ball-and-socket-joints.**" We may represent the movements as taking place around *three* axes, intersecting each other at right angles. The movements which can be performed at these joints may be grouped as:—(1) pendulum-like movements in any plane, (2) rotation round the long axis of the limb, and (3) circumscribing movements [circumduction], such as are made round the circumference of a sphere; the centre is in the point of rotation of the joint, while the circumference is described by the limb itself.

Limited arthrodial joints are ball joints with limited movements, and where rotation on the long axis is wanting, *e.g.*, the metacarpo-phalangeal joints.

5. **Rigid joints** or **amphiarthroses** are characterised by the fact that movement may occur in all directions, but only to a very limited extent, in consequence of the tough and unyielding external ligaments. Both articular surfaces are usually about the same size, and are nearly plane surfaces, *e.g.*, the articulations of the carpal and the tarsal bones.

II. **Symphyses, synchondroses**, and **syndesmoses** unite bones without the formation of a

proper articular cavity, are movable in all directions, but only to the slightest extent. Physiologically they are closely related to amphiarthrodial joints.

III. **Sutures** unite bones without permitting any movement. The physiological importance of the suture is that the bones can still grow at their edges, which thus renders possible the distention of the cavity enclosed by the bones (*Herm. v. Meyer*).

306. **ARRANGEMENT AND USES OF MUSCLES.**—The muscles form 45 per cent. of the total mass of the body, those of the right side being heavier than those on the left. Muscles may be arranged in the following groups, as far as their mechanical actions are concerned:—

A. **Muscles without a definite origin and insertion:**—

1. **The hollow muscles** surrounding globular, oval, or irregular cavities, such as the urinary bladder, gall-bladder, uterus, and heart; or the walls of more or less cylindrical canals (intestinal tract, muscular gland-ducts, ureters, Fallopian tubes, vasa deferentia, blood-vessels, lymphatics). In all these cases the muscular fibres are arranged in several layers, *e.g.*, in a longitudinal and a circular layer, and sometimes also in an oblique layer. All these layers act together and thus diminish the cavity. It is inadmissible to ascribe different mechanical effects to the different layers, *e.g.*, that the circular fibres of the intestine narrow it, while the longitudinal dilate it. Both sets of fibres rather seem to act simultaneously, and diminish the cavity by making it narrower and shorter at the same time. The only case where muscular fibres may act in partially dilating the cavity is when, owing to pressure from without, or from partial contraction of some fibres, a fold, projecting into the lumen, has been formed. When the fibres, necessarily stretching across the depression thereby produced, contract, they must tend to undo it, *i.e.*, enlarge the cavity. The various layers are all innervated from the same motor source, which supports the view of their conjoint action.

2. **The sphincters** surround an opening or a short canal, and by their action they either constrict or close it, *e.g.*, the following "sphincter muscles":—sphincter pupillæ, palpebrarum, oris, pylori, ani, cunni, urethræ.

B. **Muscles with a definite origin and insertion:**—

1. **The origin is completely fixed** when the muscle is in action. The course of the muscular fibres, as they pass to where they are inserted, permits of the insertion being approximated in a straight line towards their origin during contraction, *e.g.*, the attolens, attrahens, and retrahentes of the outer ear, and the rhomboidei. Some of these muscles are inserted into soft parts which necessarily must follow the line of traction, *e.g.*, the azygos uvulæ, levator palati mollis, and most of the muscles which arise from bone and are inserted into the skin, such as the muscles of the face, styloglossus, stylopharyngeus, &c.

2. **Both Origin and Insertion movable.**—In this case the movements of both points are inversely as the resistance to be overcome. The resistance is often voluntary, which may be increased either at the origin or insertion of the muscle. Thus, the sternocleidomastoid may act either as a depressor of the head or as an elevator of the chest; the pectoralis minor may act as an abductor and depressor of the shoulder, or as an elevator of the 3rd to 5th ribs (when the shoulder girdle is fixed).

3. **Angular Course.**—Many muscles having a fixed origin are diverted from their straight course; either their fibres or their tendons may be *bent* out of the straight course. Sometimes the curving is slight, as in the occipito-frontalis and levator palpebræ superioris, or the tendon may form *an angle* round some bony process, whereby the muscular traction acts in quite a different direction, *i.e.*, as if the muscle acted directly from this process upon its point of insertion, *e.g.*, the obliquus oculi superior, tensor tympani, tensor veli palatini, obturator internus.

4. Many of the muscles of the extremities act upon the **long bones as upon**

levers:—(*a*) Some act upon a lever with **one arm**, in which case the insertion of the muscle (power) and the weight lie upon one side of the fulcrum or point of support, *e.g.*, biceps, deltoid. The insertion (or power) often lies very close to the fulcrum. In such a case, the *rapidity* of the movement at the end of the lever is greatly increased, but force is lost [*i.e.*, what is gained in rapidity is lost in power]. This arrangement has this advantage, that, owing to the slight contraction of the muscle, little energy is evolved, which would be the case had the muscular contraction been more considerable (§ 300, I., 3). (*b*) The muscles act upon the bones as upon a lever with **two arms**, in which case the power (insertion of the muscle) lies on the other side of the fulcrum opposite to the weight, *e.g.*, the triceps and muscles of the calf. In both cases, the muscular force necessary to overcome the resistance is estimated by the principles of the lever: equilibrium is established when the static moments (=product of the power in its vertical distance from the fulcrum) are equal; or when the power and weight are inversely proportional, as their vertical distance from the fulcrum.

[**The Bony Levers.**—All the three orders of levers are met with in the body. Indeed, in the elbow-joint all the three orders are represented. The annexed scheme shows the relative positions of P, W, and F (fig. 424). The first order represented by such a movement as nodding the head, the second by raising the body on the tiptoes by the muscles of the calf, and the third by the action of the biceps in raising the fore-arm. At the elbow-joint, the first order is illustrated by extending the flexed fore-arm on the upper arm, as in striking a blow on the table, where the triceps attached to the olecranon is the power, the trochlea the fulcrum, and the hand the weight. If the hand rest on the table and the body be raised on it, then the hand is the fulcrum, while the triceps is the power raising the humerus and the parts resting on it (W). The third order has already been referred to, *e.g.*, flexing the fore-arm.]

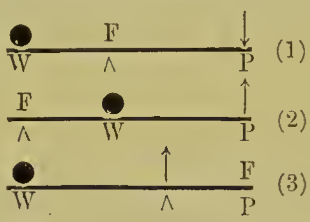


Fig. 424.
The three orders of levers.

Direction of Action.—It is most important to observe the *direction* in which the muscular force and weight act upon the lever-arm. Thus, the direction may be vertical to the lever in

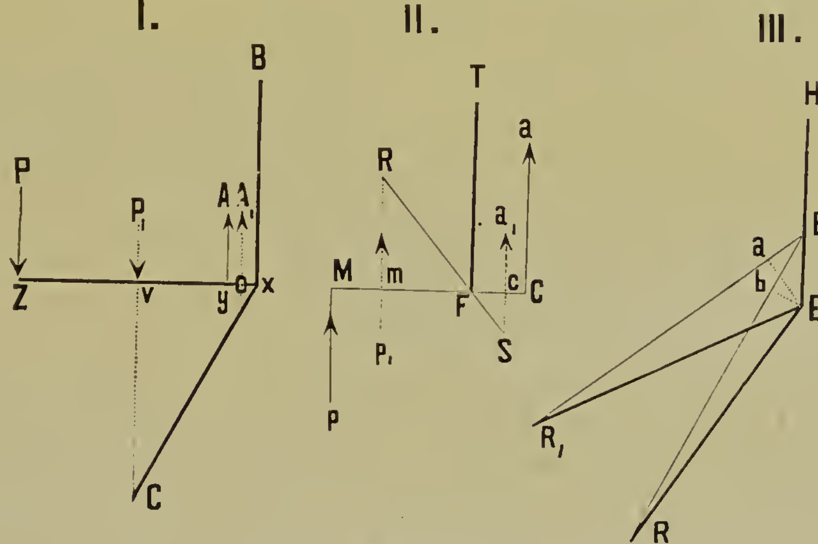


Fig. 425.
Scheme of the action of the muscles on bones.

one position, while after flexion it may act obliquely upon the lever. The static moment of a power acting *obliquely* on the lever-arm is obtained by multiplying the power with the power acting in a direction vertical to the point of rotation.

Examples:—In fig. 425 I., B x represents the humerus, and x Z the radius; A y, the direction of the traction of the biceps. If the biceps acts at a right angle only, as by lifting

horizontally a weight (P) lying on the fore-arm or in the hand, then the power of the biceps (= A) is obtained from the formula, A $y\ x$ = P x Z, *i.e.*, A = (P x Z) : $y\ x$. It is evident that, when the radius is depressed to the position x C, the result is different; then the force of the biceps = A_1 = (P_1 $v\ x$) : $o\ x$. In fig. 425, II., TF is the tibia, F, the ankle-joint, MC, the foot in a horizontal position. The power of the muscles of the calf (= a) necessary to equalise a force, p, directed from below against the anterior part of the foot, would be a=(p M F) : F C. If the foot be altered to the position R S, the force of the muscles of the calf would then be a_1=(p_1 M F) : F C.

In muscles also, which, like the coraco-brachialis are stretched over the angle of a hinge, the same result obtains.

In fig. 425, III., H E is the humerus, E, the elbow-joint, E R, the radius, B R, the coraco-brachialis. Its moment in this position is = A, a E. When the radius is raised to E R_1, then it is = A, a E. We must notice, however, that B R_1 < B R. Hence, the absolute muscular force must be less in the flexed position, because every muscle, as it becomes shorter, lifts less weight. What is lost in power is gained by the elongation of the lever-arm.

5. Many muscles have a **double action**; when contracted in the ordinary way they execute a combined movement, *e.g.*, the biceps is a flexor and supinator of the fore-arm. If one of these movements be prevented by the action of other muscles, the muscle takes no part in the execution of the other movement.

If the fore-arm be strongly pronated and flexed in this position, the biceps takes no part therein; or, when the elbow-joint is rigidly supinated, only the supinator brevis acts, not the biceps. The muscles of mastication are another example. The masseter elevates the lower jaw, and at the same time pulls it forward. If the depressed jaw, however, be strongly pulled backwards when the jaw is raised, the masseter is not concerned. The temporal muscle raises the jaw, and at the same time pulls it backwards. If the depressed jaw be raised after being pushed forward, then the temporal is not concerned in its elevation.

6. **Muscles acting on two or more joints** are those which, in their course from their origin to their insertion, pass over two or more joints. Either the tendons may deviate from a straight course, *e.g.*, the extensors and flexors of the fingers and toes, as when the latter are flexed; or the direction is always straight, *e.g.*, the gastrocnemius. The muscles of this group present the following points of interest—(*a*) The phenomenon of so-called "**active insufficiency.**" If the position of the joints over which the muscle passes be so altered that its origin and insertion come too near each other, the muscle may require to contract so much before it can act on the bones attached to it, that it cannot contract actively any further than to the extent of the shortening from which it begins to be active; *e.g.*, when the knee-joint is bent, the gastrocnemius can no longer produce plantar flexion of the foot, but the traction on the tendo Achillis is produced by the soleus. (*b*) "**Passive insufficiency**" is shown by many jointed muscles under the following circumstances:—In certain positions of the joint, a muscle may be so stretched that it may act like a rigid strap, and thus limit or prevent the action of other muscles, *e.g.*, the gastrocnemius is too short to permit complete dorsal flexion of the foot when the knee is extended. The long flexors of the leg, arising from the tuber ischii, are too short to permit complete extension of the knee-joint when the hip-joint is flexed at an acute angle. The extensor tendons of the fingers are too short to permit of complete flexion of the joints of the fingers when the hand is completely flexed.

7. **Synergetic muscles** are those which together subserve a certain kind of movement, *e.g.*, the flexors of the leg, the muscles of the calf, and others. The abdominal muscles act along with the diaphragm in diminishing the abdomen during straining, while the muscles of inspiration or expiration, even the different origins of one muscle, or the two bellies of a biventral muscle, may be regarded from the same point of view.

Antagonistic muscles are those which, during their action, have exactly the opposite effect of other muscles, *e.g.*, flexors and extensors—pronators and supina-

tors—adductors and abductors—elevators and depressors—sphincters and dilators—inspiratory and expiratory.

When it is necessary to bring the full power of our muscles into action we quite involuntarily bring them beforehand into a condition of the greatest tension, as a muscle in this condition is in the most favourable position for doing work (§ 300, I., 3). Conversely, when we execute delicate movements requiring little energy, we select a position in which the corresponding muscle is already shortened.

All the fasciæ of the body are connected with muscles, which, when they contract, alter the tension of the former, so that they are in a certain sense aponeuroses or tendons of the latter (*K. Bardeleben*). [For the importance of muscular movements and those of fasciæ in connection with the movements of the lymph, see § 201.]

307. GYMNASTICS; MOTOR PATHOLOGICAL VARIATIONS.—**Gymnastic exercise** is most important for the proper development of the muscles and motor power, and it ought to be commenced in both sexes at an early age. Systematic muscular activity increases the volume of the muscles, and enables them to do more work. The amount of blood is increased with increase in the muscular development, while at the same time the bones and ligaments become more resistant. As the circulation is more lively in an active muscle, gymnastics favour the circulation, and ought to be practised, especially by persons of sedentary habits, who are apt to suffer from congestion of blood in abdominal organs (*e.g.*, hæmorrhoids), as it favours the movement of the tissue juices [§ 201]. An active muscle also uses more O and produces more CO_2, so that respiration is also excited. The total increase of the metabolism gives rise to the feeling of well-being and vigour, diminishes abnormal irritability, and dispels the tendency to fatigue. The whole body becomes firmer, and specifically heavier (*Jäger*).

By **Ling's**, or the **Swedish system**, a systematic attempt is made to strengthen certain weak muscles, or groups of muscles, whose weakness might lead to the production of deformities. These muscles are exercised systematically by opposing to them resistances, which must either be overcome, or against which the patient must strive by muscular action.

Massage, which consists in kneading, pressing, or rubbing the muscles, favours the blood-stream; hence, this system may be advantageously used for such muscles as are so weakened by disease that an independent treatment by means of gymnastics cannot be adopted. [The importance of massage as a restorative practice in getting rid of the waste products of muscular activity has been already referred to (§ 304).]

Disturbances of the normal movements may partly affect the **passive motor organs** (*e.g.*, the bones, joints, ligaments, and aponeuroses), or the **active organs** (muscles with their tendons, and motor nerves).

Passive Organs.—Fractures, caries and necrosis, and inflammation of the bones, which make movements painful, influence or even make movement impossible. Similarly, dislocations, relaxation of the ligaments, arthritis, or anchylosis interfere with movement. Also curvature of bones, hyperostosis or exostosis; lateral curvature of the vertebral column (**Scoliosis**), backward angular curvature (**Kyphosis**), or forward curvature (**Lordosis**). The latter interfere with respiration. In the lower extremities, which have to carry the weight of the body, **genu valgum** may occur in flabby, tall, rapidly-growing individuals, especially in some trades, *e.g.*, in bakers. The opposite form, **genu varum**, is generally a result of rickets. **Flat foot** depends upon a depression of the arch of the foot, which then no longer rests upon its three points of support. Its causes seem to be similar to those of genu valgum. The ligaments of the small tarsal joints are stretched, and the long axis of the foot is usually directed outwards; the inner margin of the foot is more turned to the ground, while pain in the foot and malleoli make walking and standing impossible. Club-foot (**Talipes varus**), in which the inner margin of the foot is raised, and the point of the toes is directed inwards and downwards, depends upon imperfect development during fœtal life. All children are born with a certain very slight degree of bending of the foot in this direction. **Talipes equinus**, in which the toes, and **T. calcaneus**, in which the heel touches the ground, usually depend upon contracture of the muscles causing these positions of the foot, or upon paralysis of the antagonistic muscles.

Rickets and Osteomalacia.—If the earthy salts be withheld from the food, the bones gradually undergo a change; they become thin, translucent, and may even bend under pressure. In certain persistent defects of nutrition, the lime and other salts of the food are not absorbed, giving rise to **rachitis**, or rickets, in children. If fully formed bones lose their lime-salts to the extent of ½ to ⅓ (**halisterisis**), they become brittle and soft (**osteomalacia**). This occurs to a limited extent in old age.

Muscles.—The normal nutrition of muscle is intimately dependent on a proper supply of *sodium chloride and potash salts* in the food, as these form integral parts of the muscular tissue (*Kemmerich, Forster*). Besides the atrophic changes which occur in the muscles when these substances are withheld, there are disturbances of the central nervous system and digestive apparatus, and the animals ultimately die. The condition of the muscles during inanition is given in § 237. If muscles and bones be kept inactive, they tend to atrophy (§ 244). In atrophic muscles, and in cases of anchylosis, there is an enormous increase, or "atrophic proliferation," of the muscle-corpuscles, which takes place at the expense of the contractile contents (*Cohnheim*). A certain degree of muscular atrophy takes place in old age. The **uterus**, after delivery, undergoes a great decrease in size and weight—from 1000 to 350 grams—due chiefly to the diminished blood-supply to the organ. In chronic *lead poisoning*, the extensors and interossei chiefly undergo atrophy. Atrophy and degeneration of the muscles are followed by shortening and thinning of the bones to which the muscles are attached.

Section and paralysis of the motor nerves cause palsy of the muscles, thus rendering them inactive, and they ultimately degenerate. Atrophy also occurs after inflammation or softening of the **multipolar nerve-cells** in the anterior horn of the grey matter of the spinal cord, or the *motor nuclei* (facial, spinal accessory, and hypoglossal of Stilling in the medulla oblongata), in the muscles connected with these parts. Rapid atrophy takes place in certain forms of spinal paralysis and in acute bulbar paralysis (paralysis of the medulla oblongata), and in a chronic form in progressive muscular atrophy and progressive bulbar paralysis. The muscles and their nerves become small and soft. The muscles show many nuclei, the sarcous substance becomes fatty, and ultimately disappears. According to Charcot, these areas are at the same time the trophic centres for the nerves proceeding from them, as well as for the muscles belonging to them. According to Friedreich, the primary lesion in progressive muscular atrophy is in the muscles, and is due to a primary interstitial inflammation of the muscle, resulting in atrophy and degenerative changes, while the nerve-centres are affected secondarily, just as after amputation of a limb, the corresponding part of the spinal cord degenerates.

In **pseudo-hypertrophic muscular atrophy** the muscular fibres atrophy completely, with copious development of fat and connective-tissue between the fibres, without the nerves or spinal cord undergoing degeneration. The muscular substance may also undergo *amyloid or wax-like* degeneration, whereby the amyloid substance infiltrates the tissue (§ 249, VI.). Sometimes atrophic muscles have a *deep brown colour*, due to a change of the hæmoglobin of the muscle. When muscles are much used they **hypertrophy**, as the heart in certain cases of valvular lesion or obstruction (§ 40), the bladder, and intestine. [In true **hypertrophy** there is an increased number, or increase in the size, of its tissue elements, throughout the entire tissue or organ, without any deposit of a foreign body. Perhaps, in hypertrophy of the bladder, the thickened muscular coat not only serves to overcome resistance, but it offers greater resistance to bursting under the increased intra-vesical pressure. Mere **enlargement** is not hypertrophy, for this may be brought about by foreign elements. In **atrophy** there is a diminution in size or bulk, even when the blood-stream is kept up, the decrease being due to pressure. An atrophied organ may be even enlarged, as seen in pseudo-hypertrophic paralysis, where the muscles are larger, owing to the interstitial growth of fatty and connective-tissue, while the true muscular tissue is diminished and truly atrophied.]

Special Muscular Acts.

308. STANDING.—The act of **standing** is assured by muscular action, and is the vertical position of equilibrium of the body, in which a line drawn from the centre of gravity of the body falls within the area of both feet placed upon the ground. In the military attitude, the muscles act in two directions—(1) to fix the jointed body, as it were, into one unbending column; and (2) in case of a variation of the equilibrium, to compensate by muscular action for the disturbance of the equilibrium.

The following individual motor acts occur in standing:—

1. **Fixation of the head** upon the vertebral column. The occiput may be moved in various directions upon the atlas, as in the acts of *nodding*. As the long arm of the lever lies in front of the atlas, necessarily when the muscles of the back of the neck relax, as in sleep or death, the chin falls upon the breast. The strong neck muscles, which pull from the vertebral column upon the occiput, fix the head in a firm position on the vertebral column. The chief rotatory movement of the head on a vertical axis occurs round the odontoid process of the axis. The

articular surfaces on the pedicles, and part of the bodies of the 1st and 2nd vertebræ, are convex towards each other in the middle, becoming somewhat lower in front and behind, so that the head is highest in the erect posture. Hence, when the head is greatly rotated, compression of the medulla oblongata is prevented (*Henke*). In standing, these muscles do not require to be fixed by muscular action, as no rotation can take place when the neck muscles are at rest.

2. **Fixed Vertebral Column.**—The vertebral column itself must be fixed, especially where it is most mobile, *i.e.*, in the cervical and lumbar regions. This is brought about by the strong muscles situate in these regions, *e.g.*, the cervical spinal muscles, *Extensor dorsi communis* and *Quadratus lumborum.*

Mobility of the Vertebræ.—The least movable vertebræ are the 3rd to the 6th dorsal; the sacrum is quite immovable. For a certain length of the column the mobility depends on (*a*) the number and height of the interarticular fibro-cartilages. They are most numerous in the neck, thickest in the lumbar region, and relatively also in the lower cervical region. They permit movement to take place in every direction. Collectively the interarticular discs form one-fourth of the height of the whole vertebral column. They are compressed somewhat by the pressure of the body; hence, the body is longest in the morning and after lying in the horizontal position. The smaller periphery of the bodies of the cervical vertebræ favours the mobility of these vertebræ compared with the larger lower ones. (*b*) The position of the processes also influences greatly the mobility. The strongly depressed spines of the dorsal region hinder hyperextension. The articular processes on the cervical vertebræ are so placed that their surfaces look obliquely from before and upwards, backwards, and downwards; this permits relatively free movement, rotation, lateral and nodding movements. In the dorsal region, the articular surfaces are directed vertically and directly to the front, the lower directly backwards; in the lumbar region the position of the articular processes is almost completely vertical and antero-posterior. In bending backwards as far as possible, the most mobile parts of the column are the lower cervical vertebræ, the 11th dorsal to the 2nd lumbar, and the lower two lumbar vertebræ (*E. H. Weber*).

3. The centre of gravity of the head, trunk, and arms when fixed as above, lies in front of the 10th dorsal vertebra. It lies further forward, in a horizontal plane, passing through the xiphoid process, the greater the distension of the abdomen by food, fat, or pregnancy. A line drawn vertically downwards from the centre of gravity passes *behind* the line uniting both hip-joints. Hence, the trunk would fall backwards on the hip-joint, were it not prevented partly by ligaments and partly by muscles. The former are represented by the ileo-femoral band and the anterior tense layer of the fascia lata. As ligaments alone, however, never resist permanent traction, they are aided, especially by the ileo-psoas muscle inserted into the small trochanter, and in part, also, by the rectus femoris. Lateral movement at the hip-joint, whereby the one limb must be abducted and the other adducted, is prevented especially by the large mass of the glutei. When the leg is extended, the ileo-femoral ligament, aided by the fascia lata, prevents adduction.

4. The rigid part of the body, head, and trunk, with the arms and legs, whose centre of gravity lies lower and only a little in front, so that the vertical line drawn downwards intersects a line connecting the posterior surfaces of the knee-joints, must now be fixed at the knee-joint. Falling backwards is prevented by a slight action of the quadriceps femoris, aided by the tension of the fascia lata. Indirectly it is aided also by the ileo-femoral ligament. Lateral movement of the knee is prevented by the disposition of the strong lateral ligaments. Rotation cannot take place at the knee-joint in the extended position (§ 305, I., 3).

5. A line drawn downwards from the centre of gravity of the whole body, which lies in the promontory, falls slightly in front of a line between the two ankle-joints. Hence, the body would fall *forward* on the latter joint. This is prevented especially by the muscles of the calf, aided by the muscles of the deep layer of the leg (tibialis posticus, flexors of the toes, peroneus longus et brevis).

Other Factors:—(*a*) As the long axis of the foot forms with the leg an angle of 50°, falling forward can only occur after the feet are in a position more nearly parallel with their long axis. (*b*) The form of the articular surfaces helps, as the anterior broad part of the astragalus must be pressed between the two malleoli. The latter mechanism cannot be of much importance.

6. The metatarsus and phalanges are united by tense ligaments to form the arch of the foot, which touches the ground at three points—tuber calcanei (heel), the head of the first metatarsal bone (ball of the great toe), and of the fifth toe. Between the latter two points, the heads of the metatarsal bones also form points of support. The weight of the body is transmitted to the highest part of the arch of the foot, the caput tali. The arching of the foot is fixed only by ligaments. The toes play no part in standing, although, when moved by their muscles, they greatly aid the balancing of the body. The maintenance of the erect attitude fatigues one more rapidly than walking.

309. SITTING.—Sitting is that position of equilibrium whereby the body is supported on the tubera ischii, on which a to and fro movement may take place

(*H. v. Meyer*). The head and trunk together are made rigid to form an immovable column, as in standing.

We may distinguish—(1) the **forward posture**, in which the line of gravity passes in front of the tubera ischii; the body being supported either against a fixed object, *e.g.*, by means of the arm on a table, or against the upper surface of the thigh. (2) The **backward posture**, in which the line of gravity falls behind the tubera. A person is prevented from falling backward either by leaning on a support, or by the counter-weight of the legs kept extended by muscular action, whereby the sacrum forms an additional point of support, while the trunk is fixed on the thigh by the ileo-psoas and rectus femoris, the leg being kept extended by the extensor quadriceps. Usually the centre of gravity is so placed that the heel also acts as a point of support. The latter sitting posture is of course not suited for resting the muscles of the lower limbs. (3) When "**sitting erect**" the line of gravity falls between the tubera themselves. When the muscles of the legs are relaxed, the rigid trunk only requires to be balanced by slight muscular action. Usually the balancing of the head is sufficient to maintain the equilibrium.

310. WALKING, RUNNING, AND SPRINGING.

—By the term **walking** is understood progression in a forward horizontal direction with the least possible muscular exertion, due to the alternate activity of the two legs.

Methods.—The Brothers Weber were the first to analyse the various positions of the body in walking, running, and springing, and they represented them in a *continuous series*, which represents the successive phases of locomotion. These phases may be examined with the zoetrope (§ 398, 3). Marey estimated the *time-relations* of the individual acts by transferring the movements by means of his air-tambours to a recording surface. Recently, by means of a revolving camera, he has succeeded in **photographing**, in instantaneous pictures ($\frac{1}{700}$ second), the whole series of acts. Of course this series, when placed in the zoetrope, represents the natural movements. Figs. 427, 428, 429 represent these acts.

In **walking**, the legs are active alternately; while one—the "supporting" or "active" leg—carries the trunk, the other is "inactive" or "passive." Each leg is alternately in an active and a passive phase. Walking may be divided into the following movements:—

I. Act (fig. 426, 2).—The *active* leg is vertical, slightly flexed at the knee, and it alone supports the centre of gravity of the body. The passive leg is completely extended, and touches the ground only with the tip of the great toe (z). This position of the leg corresponds to a right-angled triangle, in which the active leg and the ground form two sides, while the passive leg is the hypothenuse.

Fig. 426.

Phases of walking. The thick lines represent the active, the thin the passive leg; h, the hip-joint; k, a, knee; f, b, ankle; c, d, heel; m, e, ball of the tarso-metatarsal joint; z, g, point of great toe.

II. Act.—For the forward movement of the trunk, the active leg is inclined slightly from its vertical position (cathetus) to an oblique and more forward (hypothenuse) position (3). In order that the trunk may remain at the same height, it is necessary that the active leg be lengthened. This is accomplished by completely extending the knee (3, 4, 5), as well as by lifting the heel from the ground (4, 5), so that the foot rests on the balls or the heads of the metatarsal bones, and, lastly, by elevating it on the point of the great toe (2, thin line). *During* the extension and forward movement of the active leg, the tips of the toes of the passive leg have left the ground (3). It is slightly flexed at the knee-joint (owing to the shortening), it performs a "pendulum-like movement" (4, 5), whereby its foot is moved as far in front of the active leg as it was formerly behind it. The foot is then placed flat upon the ground (1, 2, thick lines); the centre of gravity is now transferred to this active leg, which at the same time is slightly flexed at the knee, and placed vertically. The first act is then repeated.

Simultaneous Movements of the Trunk.—During walking the trunk performs certain characteristic movements. (1) It leans every time towards the active leg, owing to the traction of the glutei and the tensor fasciæ latæ, so that the centre of gravity is moved, which in short heavy persons with a broad pelvis leads to their "waddling" gait. (2) The trunk, especially during rapid walking, is inclined slightly forward to overcome the resistance of the air. (3)

Fig. 427.

Phases of slow walking. Instantaneous photograph; only the side directed to the observer is shown. From the vertical position of the right, active leg; (I.), all the phases of this leg are represented in six pictures (I. to VI.), while after VI. the vertical position is regained. The Arabic numerals indicate the simultaneous position of the corresponding left leg; thus 1 = I., 2 = II., &c., so that during the position IV. of the right leg, at the same time the left leg has the position as 1.

During the "pendulum-like action," the trunk rotates slightly on the head of the active femur. This rotation is compensated, especially in rapid walking, by the arm of the same side as the oscillating leg swinging in the opposite direction, while that on the other side at the same time swings in the same direction as the oscillating limb.

Modifying Conditions: 1. *The Duration of the Step.*—As the rapidity of the vibration of a pendulum (leg) depends upon its length, it is evident that each individual, according to the length of his legs, must have a certain natural rate of walking. The "*duration of a step*" depends also upon the time during which both feet touch the ground simultaneously, which, of course, can be altered voluntarily. When "walking rapidly" the time = 0, *i.e.*, at the same moment in which the active leg reaches the ground, the passive leg is raised. *The length*

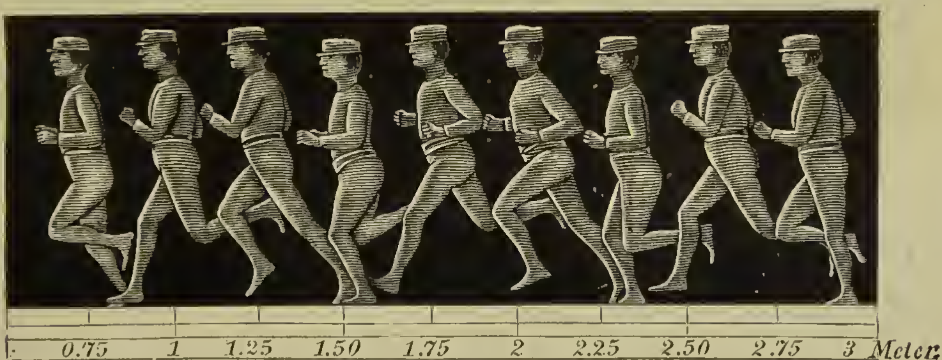


Fig. 428.

Instantaneous photograph of a runner. Ten pictures per second. The abscissa indicates the length of the step in metres.

of the step is usually about 6 to 7 decimetres [23 to 27 inches], and it must be greater the more the length of the hypothenuse of the passive leg exceeds the cathetus of the active one. Hence, during a long step, the active leg is greatly shortened (by flexion of the knee), so that the trunk is pulled downwards. Similarly, long legs can make longer steps.

According to Marey and others, the **pendulum movement** of the passive leg is not a true pendulum movement, because its movement, owing to muscular action, is of more uniform rapidity. During the pendulum movement of the whole limb, the leg vibrates by itself at the knee-joint (*Lucæ, H. Vierordt*).

Fixation of the Femur.—According to Ed. and W. Weber, the head of the femur of the passive leg is fixed in its socket chiefly by the **atmospheric pressure,** so that no muscular action is necessary for carrying the whole limb. If all the muscles and the capsule be divided, the head of the femur still remains in the cotyloid cavity. Rose refers this condition not to the action of the atmospheric pressure, but to two adhesion surfaces united by means of synovia. The experiments of Aeby show that not only the weight of the limb is supported by the atmospheric pressure, but that the latter can support several times this weight. When traction is exerted on the limb, the margins of the cotyloid ligament of the cotyloid cavity are applied like a valve tightly to the margin of the cartilage of the head of the femur. According to the Brothers Weber, the leg falls from its socket as soon as air is admitted by making a perforation into the articular cavity.

Work done during Walking.—Marey and Demery estimate the amount done by a man weighing 64 kilos. [10 stones], when walking slowly, as = 6 kilogrammetres per second ; rapid running = 56 kilogrammetres. The work done is due to the raising of the entire body and extremities, to the velocity communicated to the body, as well as to the maintenance of the centre of gravity.

In **springing** or **leaping**, the body is rapidly projected upwards by the greatest possible and most rapid contraction of the muscles, while at the same time the centre of gravity is maintained by other muscular acts (fig. 429).

The **pressure** upon the sole of the foot in walking is distributed in the following manner:—The supporting leg always presses more strongly on the ground than the other ; the longer the step the greater the pressure. The heel receives the maximum amount of pressure sooner than the point of the foot (*Carlet*).

Running is distinguished from rapid walking by the fact that, at a particular

Fig. 429.

High leap. Instantaneous photograph. The pictures partly overlap each other, as soon as the velocity of the forward movement on the descent diminishes after springing. In the left-hand corner is the dial plate, the radius of which moved one division in $\frac{1}{12}$ second. The abscissa indicates the distance in metres.

moment, both legs do not touch the ground, so that the body is raised in the air. The active leg, as it is forcibly extended from a flexed position, gives the body the necessary impetus (fig. 429).

Pathological.—Variations of the walking movements depend primarily upon diseases of bones, ligaments, muscles, and tendons, and also upon affections of the motor nerves. The effect of sensory nerves and the reflex mechanism of the spinal cord, and also of the muscular sense on walking, are stated in §§ 355, 360, 430.

311. COMPARATIVE.—The **absolute muscular force** in animals is not, as a rule, much different from that in man. The great motor power exerted by animals results from the **thickness** and **number** of the muscles, as well as from the different arrangement of the levers and the action of muscles on them. Insects particularly

exert a large amount of force; some insects can drag a body sixty-seven times their own weight; a horse scarcely its own weight. A man pressing upon a dynamometer with one hand exerts pressure = 0·70 times his own weight, while a dog lifting its lower jaw exerts 8·3 times; a crab by closing its pincers 28·5 times; and a mussel on closing its shell 382 times its body-weight (*Plateau*).

In mammals standing is much more easy, as they have four supporting surfaces. The springing animals have a sitting attitude, while the tail is often used as a support (kangaroo, squirrel). In **birds** there is a mechanical arrangement by which, while perching, the tendons are flexed; hence, a bird while sleeping can still retain its hold (*Cuvier*). In the stork and crane, which stand for a long time on one leg, this act is unaccompanied by muscular action, as the tibia is fixed by means of a process which fits into a depression of the articular surface of the femur.

In **walking**, we distinguish in mammals the **step** (le pas)—the four feet are generally moved in four tempo, and usually diagonally, *e.g.*, in the horse right fore, left hind; left fore, right hind. [The camel is an exception—it moves the fore and hind limbs simultaneously on each side]. In **trotting** this movement is accelerated; the two limbs in a diagonal direction lift together, so that only two hoof-sounds are heard, while at the same time the body is raised more in the air. During the interval between two hoof-beats the body is free in the air, all the limbs having left the ground. Strictly speaking, the fore limb leaves the ground slightly sooner than the hind one. The **gallop.**—When a (right) galloping horse moves in the air, the upper part of its body is fairly horizontal; when it touches the ground, the left hind foot is the first to touch the ground. Shortly thereafter, the left fore and right hind foot touch the ground, while the right fore leg has not yet reached the ground and is directed forward. The upper part of the body still retains its horizontal direction. When, however, a few moments thereafter the left hind leg again leaves the ground, it is higher than the fore leg—simultaneously the right fore leg is thrown forward and lower, while the right hind and left fore leg are stretched to the extreme. Immediately thereafter these limbs leave the ground, while the hind limb so far overtakes the fore limb that it comes to lie higher than the latter. The body, therefore, is projected forwards and downwards until the right fore limb, which alone touches the ground, actively contracts and again raises the body from the ground. When this happens, the horse again moves in the air, its body being directed horizontally. The long axis of the horse's body in galloping is placed obliquely to the direction of movement, and forming a right angle. In forced galloping (la carrière), which is really a springing movement, the right hind leg and left fore leg do not touch the ground at the same time, but the former does so sooner. The **amble** is a modification of the step, which consists in this, that both feet on the *same* side move at the same time or shortly after each other (camel, giraffe, elephant). Marey attached compressible ampullæ under the hoof of a horse, connecting them with registering apparatus, and thus accurately registered the time relation of each act. Muybridge photographed the actions of a horse and the different phases of the movement.

In **snakes** the rudder-like elevation and depression of the ribs cause the progression of the body.

Swimming is an acquired art in **man**. The specific gravity of the body is slightly greater than that of ordinary water, but slightly lighter than that of sea water. When lying quietly on the back, so that only the mouth and nose are at last above the water, very slight movements of the hands are necessary to keep a person from sinking. In this position, progression can be accomplished by extending and adducting the legs, while the movement is accelerated by rudder-like movements of the arms. Swimming belly downwards is more difficult, because the head being held above the water makes the body specifically heavier. The forward movement and the act of supporting the body in the water consist of three acts:—*First*, horizontal, rudder-like movements of the extended arms from before backwards, until they reach the horizontal position (forward movement); *second*, pressure of the arms downward with subsequent adduction of the elbow-joint to the body (elevation of the body), together with retraction of the extended legs; *third*, projection of the arms, now brought together, and at the same time extension and adduction of the legs obliquely backwards and downwards, thus causing elevation of the body as well as a forward movement. Too rapid movements cause fatigue, while the respirations must be carefully regulated. Many **land mammals**, whose body is specifically lighter than water, can swim, especially with the aid of their hind limbs, while at the same time all the legs being directed downwards, and being specifically the heaviest part of the body, keep the trunk in the normal position. **Fishes** chiefly use their tail fin as a motor organ, which is moved by powerful lateral muscles. When the tail is suddenly extended, it presses upon the water and displaces it. Some fish, as the salmon, can lift their body out of the water by a blow of their tail fin. The dorsal and anal fins enable the animal to preserve the erect position. The pectoral and abdominal fins corresponding to the extremities execute slight movements, especially upwards and downwards, which are greater during sleep. The **swimming-bladder** is the homologue of the lung, and is used for hydrostatic purposes in some fishes, and as an

auxiliary respiratory organ in others, *e.g.*, the dipnoi (§ 140). It is absent or rudimentary in the cyclostomata. In **swimming birds**, the body is specifically very much lighter than the water, while their feathers are lubricated by the oily secretion of the coccygeal glands (§ 291). Their feet are usually webbed.

Flight.—Bats and their allies are the only flying mammals. The bones of the upper limb and phalanges are greatly elongated, and between these and the elongated hind limb (except the foot) there is stretched a thin membrane. The membrane is moved by the powerful pectoral muscles. The flying squirrel has only a duplicature of the skin stretched between the large bones of the extremities, which serves as a parachute when the animals spring. In **birds** the body is specifically light; numerous air-sacs in the chest and belly communicate with the lungs, and with the cavities of most of the bones (§ 140). The modified upper extremities are supported by the coracoid bone and the united clavicles or furculum, and are moved by the powerful pectoral muscles attached to the keeled sternum. Marey, by means of his revolving photographic camera, has analysed all the phases of flight in a bird.

[Warner has studied the **movements of the fingers**, and correlated these movements with changes in the nerve-centres in certain diseased conditions, *e.g.*, chorea. An india-rubber tube is attached to each finger, and this "motor" part of the apparatus is connected with a Marey's tambour. The several finger-tubes are fixed to an arrangement not unlike a cricketer's glove, so that voluntary or involuntary movements of the fingers can be registered and studied.]

Voice and Speech.

312. VOICE, PHYSICAL CONSIDERATIONS.—The blast of **expired air**—and under certain circumstances, the inspiratory blast also—is employed to throw the tense **vocal cords** into a state of regular vibration, whereby a sound is produced. The sound so produced is the human voice.

The **true vocal cords** are really elastic "membranous" reeds. If a blast of air be forcibly driven upwards through the partially closed glottis, the vocal cords are pushed asunder, as the elastic tension of the air overcomes the resistance of the cords. After the escape of air from below, the cords rapidly return to their former position, and are again pushed asunder, and caused to vibrate.

1. Thus, when a membrane vibrates, the air must be alternately condensed and rarefied. The condensation and rarefaction are the chief cause of the tone or note (as in the siren), not so much the membranes themselves (*v. Helmholtz*).

2. The **air-tube** or "**porte vente**," conducting the air to the membranes in man is the lower portion of the larynx, the trachea, and the whole bronchial system; the **bellows** are represented by the chest and lungs, which are forcibly diminished in size by the expiratory muscles.

3. The cavities which lie above the membranes constitute "**resonators**," and consist of the upper part of the larynx, pharynx, and also of the cavities of the nose and mouth, arranged, as it were, in two stories, the one over the other, which can be closed alternately.

The **pitch of the tone** produced by a membranous apparatus depends upon the following factors:—

(*a*) On the *length* of the elastic membranes or plates. The pitch is inversely proportional to the length of the elastic membrane, *i.e.*, the shorter the membrane the higher the pitch, or the greater the number of vibrations per second. Hence, the pitch of a child's vocal cords (shorter) is higher than that of an adult.

(*b*) The pitch of the tone is directly proportional to the square root of the amount of the elasticity of the elastic membrane. In membranous reeds, and also with silk, it is directly proportional to the square root of the extending weight, which in the case of the larynx is the force of the muscle rendering the cords tense.

(*c*) The tone of membranous reeds is not only *strengthened by a more powerful blast*, as the amplitude of the vibrations is increased, but the *pitch of the tone may also be raised* at the same time, because, owing to the great amplitude of the vibration, the mean tension of the elastic membrane is increased.

(*d*) The supra-laryngeal cavities, which act as **resonators**, are also inflated when the larynx is in action, so that the tone produced by these cavities is added to and blended with the sound of the elastic membranes, whereby certain partial tones of the latter are strengthened (§ 415). The characteristic timbre of the voice largely depends upon the form of the resonators.

(*e*) When vocalising, the strongest resonance takes place in the *air-tubes*, as they contain compressed air. It causes the vocal fremitus which is audible on placing the ear over the chest (§ 117, 6).

(*f*) *Narrowing or dilating* the glottis has no effect on the pitch of the tone, only with a wide glottis much more air must be driven through it, which, of course, greatly increases the work of the thorax.

313. ARRANGEMENT OF THE LARYNX.—I. Cartilages and Ligaments.—The fundamental part of the larynx consists of the **cricoid cartilage**, whose small narrow portion is directed forwards and the broad plate backwards. The **thyroid cartilage** articulates by its inferior cornu with the posterior lateral portion of the cricoid. This permits of the thyroid cartilage rotating upon a horizontal

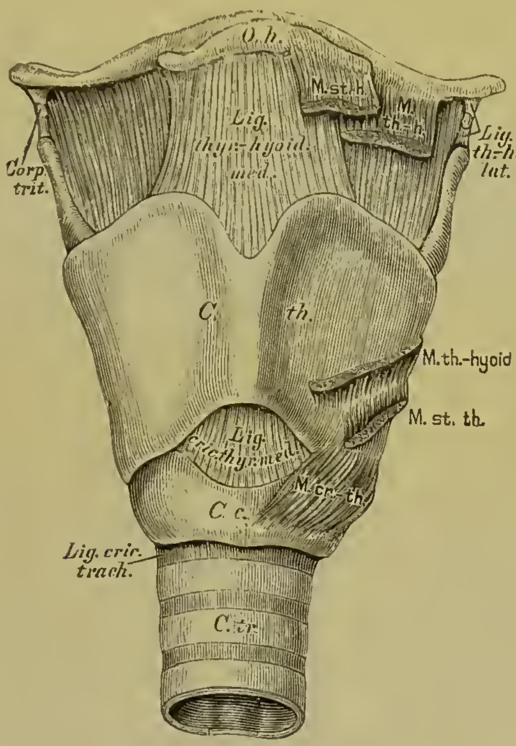


Fig. 430.

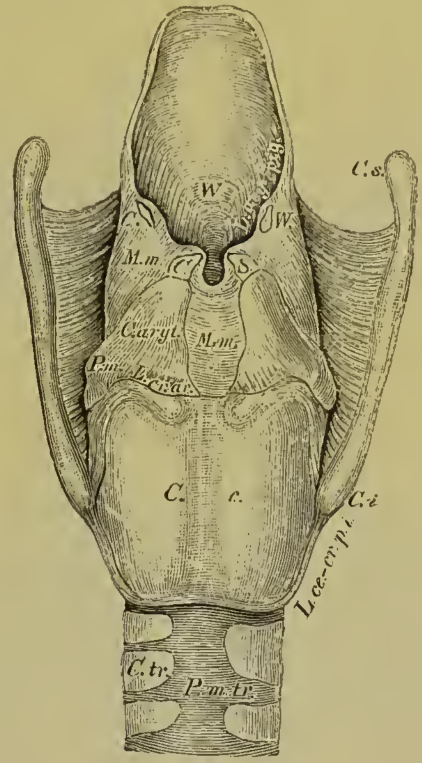


Fig. 431.

Fig. 430.—Larynx from the front, with the ligaments and the insertions of the muscles. *O.h.*, Os hyoideum ; *C.th.*, Cart. thyreoidea ; *Corp. trit.*, Corpus triticeum ; *C.c.*, Cart. cricoidea ; *C.tr.*, Cart. tracheales ; *Lig. thyr.-hyoid. med.*, Ligamentum thyreo-hyoideum medium ; *Lig. th.-h. lat.*, Ligam. thyreo-hyoideum laterale ; *Lig. cric. thyr. med.*, Ligam. crico-thyreoideum medium ; *Lig. cric.-trach.*, Ligam. crico-tracheale ; *M. st.-h.*, Musc. sterno-hyoideus ; *M. th.-hyoid.*, Musc. thyreo-hyoideus ; *M. st.-th.*, Musc. sterno-thyreo-ideus ; *M. cr.-th.*, Musc. crico-thyreoideus. Fig 431.—Larynx from behind after removal of the muscles. *E.*, Epiglottis cushion (W.) ; *L. ar.-ep.*, Lig. ary-epiglotticum ; *M.m.*, Membrana mucosa ; *C. W.*, Cart. Wrisbergii ; *C.S.*, Cart. Santorini ; *C. aryt.*, Cart. arytænoidea ; *C.c.*, Cart. cricoidea ; *P.m.*, Processus muscularis of Cart. arytæn. ; *L. cr.-ar.*, Ligam. crico-arytæn. ; *C.s.*, Cornu superius ; *C.i.*, Cornu inferius Cart. thyreoidea ; *L. ce.-cr. p. i.*, Lig. kerato-cricoideum. post. inf. ; *C.tr.*, Cart. tracheales ; *P.m.tr.*, Pars membranacea tracheæ.

axis directed through both of the articular surfaces, so that the upper margin of the thyroid passes forward and downward, while the joint is so constructed as to permit also of a slight upward, downward, forward, and backward movement of the thyroid upon the cricoid cartilage. The triangular **arytenoid cartilages** articulate at some distance from the middle line, with oval, saddle-like, articular surfaces placed upon the upper margin of the plate of the cricoid cartilage. The articular surfaces permit two kinds of movements on the part of the arytenoid cartilages; first, **rotation** on their base around their vertical long axis, whereby either the anterior angle or processus vocalis, which is directed forwards, is rotated

outwards; while the processus muscularis, which is directed outwards and projects over the margin of the cricoid cartilage, is rotated backwards and inwards, or conversely. Further, the arytenoids may be slightly **displaced** upon their bases either outwards or inwards.

The true vocal cords, or thyro-arytenoid ligaments, are in man about 15 millimetres, and in woman 11 millimetres in length, and consist of numerous elastic fibres. They arise close to each other from near the middle of the inner angle of the thyroid cartilage, and are inserted, each into the anterior angle or processus vocalis of the arytenoid cartilages. The **ventricles of Morgagni** permit free

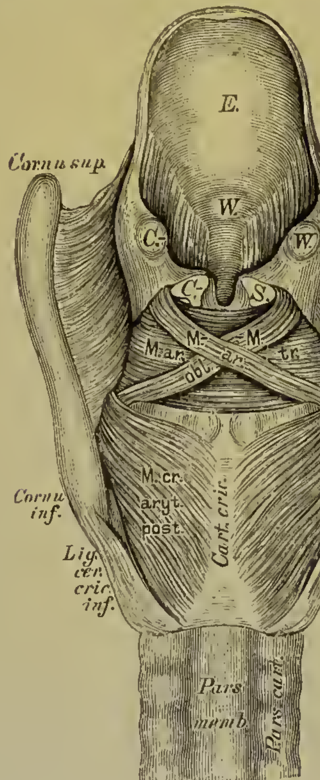


Fig. 432.

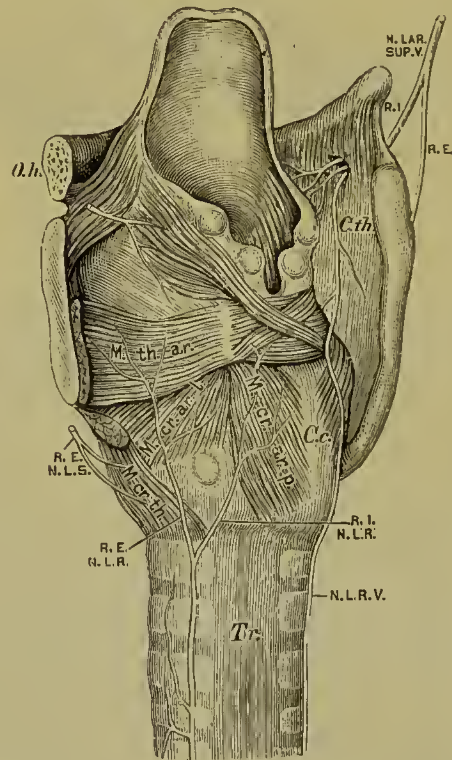


Fig. 433.

Fig. 432.—Larynx from behind with its muscles. *E.*, Epiglottis, with the cushion (W.); *C. W.*, Cart. Wrisbergii; *C.S.*, Cart. Santorini; *C.c.*, Cart. cricoidea. Cornu sup.—Cornu inf., Cart. thyreoideæ; *M. ar. tr.*, Musc. arytænoideus transversus; *Mm. ar. obl.*, Musculi arytænoidei obliqui; *M. cr. aryt. post.*, Musculus crico-arytænoideus posticus; *Pars cart.*, Pars cartilaginea; *Pars memb.*, Pars membranacea tracheæ. Fig. 433.—Nerves of the larynx. *O.h.*, Os hyoideum; *C.th.*, Cart. thyreoidea; *C.c.*, Cart. cricoidea; *Tr.*, Trachea; *M. th.-ar.*, M. thyreo-arytænoideus; *M. cr.-ar. p.*, M. crico-arytænoideus posticus; *M. cr.-ar. l.*, M. crico-arytæn. lateralis; *M. cr.-th.*, M. crico-thyreoideus; *N. lar. sup. v.*, N. laryngeus sup.; *R.I.*, Ramus internus; *R.E.*, Ramus ext.; *N. lar. rec.v.*, N. laryngeus recurrens; *R.I.N.L.R.*, Ramus int., *R.E.N.L.R.*, Ramus ext. nervi laryngei recurrentis vagi.

vibration of the true vocal cords, and separate them from the upper or false cords, which consist of folds of mucous membrane. The false vocal cords are not concerned in phonation, but the secretion of their numerous mucous glands moistens the true vocal cords.

The obliquely directed under-surface of the vocal cords causes the cords to come together very easily when the glottis is narrow during respiration (*e.g.*, in sobbing), while the closure may be made more secure by respiration. The opposite is the condition of the false vocal cords, which, when they touch, are easily separated during inspiration; while during expiration, owing to the

dilatation of the ventricles of Morgagni, they easily come together and close (*Wyllie, L. Brunton and Cash*).

II. Action of the Laryngeal Muscles.—[The representation of the movements of the larynx in the cortex cerebri is referred to under Cerebrum.] These muscles have a double function :—1. One connected with **respiration**, in as far as the glottis is widened and narrowed alternately during respiration ; further, when the glottis is firmly closed by these muscles, the entrance of foreign substances into the larynx is prevented. The glottis is closed immediately before the act of coughing (§ 120). 2. The laryngeal muscles give the vocal cords the proper tension and other conditions for **phonation**.

1. The **glottis** is **dilated** by the action of the **posterior crico-arytenoid** muscles. When they contract they pull both processus musculares of the arytenoid cartilages backwards, downwards, and towards the middle line (fig. 434), so that the processus vocales (I, I) must go apart and upwards (II, II). Thus, between the vocal cords (**glottis vocalis**), as well as between the inner margins of the arytenoid cartilages, a large triangular space is formed (**glottis respiratoria**), and these spaces are so arranged that their bases come together, so that the aperture between the cords and the arytenoid cartilages has a rhomboidal form. Fig. 434 shows the action of the muscles. The vocal cords, represented by lines converging in front, arise from the anterior angle of the arytenoid cartilages (I, I). When these cartilages are rotated into the position (II, II), the cords take the position indicated by the dotted lines. The widening of the respiratory portion of the glottis between the arytenoid cartilages is also indicated in the diagram.

Pathological.—When these muscles are paralysed, the widening of the glottis does not take place, and there may be severe dyspnœa during inspiration, although the voice is unaffected (*Reigel, L. Weber*). In a larynx just excised, the dilators are the first to lose their excitability (*Semon and Horsley*). In organic disease affecting the recurrent laryngeal nerve the branch to the posterior crico-arytenoid is first paralysed (*Semon*). When the recurrent nerve is exposed and cooled, the branch to the posterior crico-arytenoid is the first to lose its excitability (*Fränkel and Gad*).

2. The entrance to the **glottis** is **constricted** by the **arytenoid muscle** (trans-

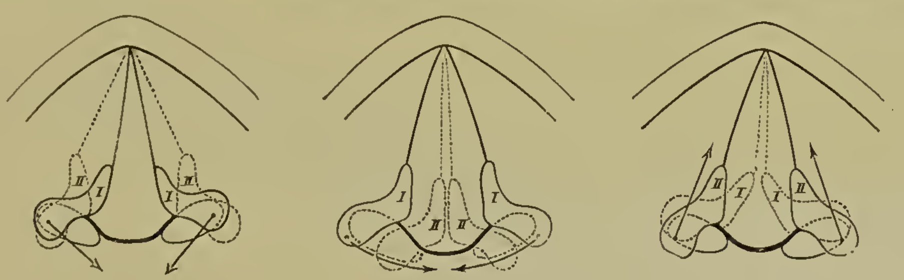


Fig. 434. Fig. 435. Fig. 436.

Fig. 434.—Schematic horizontal section of the larynx. I, Position of the horizontally divided arytenoid cartilages during respiration ; from their anterior processes run the converging vocal cords. The arrows show the line of traction of the *posterior crico-arytenoid* muscles ; II, II, the position of the arytenoid muscles, as a result of this action. Fig. 435.—Schematic horizontal section of the larynx, to illustrate the action of the *arytenoid muscle*. I, I, position of the arytenoid cartilages during quiet respiration. The arrows indicate the direction of the contraction of the muscle ; II, II, the position of the arytenoid cartilages after the arytænoideus contracts. Fig. 436.—Scheme of the closure of the glottis by the *thyro-arytenoid* muscles. II, II, position of the arytenoid cartilages during quiet respiration. The arrows indicate the direction of the muscular traction.—I, I, position of the arytenoid cartilages after the muscles contract.

verse), which extends transversely between both outer surfaces of the arytenoids along their whole length (fig. 435). On the posterior surface of this muscle is placed the cross bundles (fig. 432) of the thyro-aryepiglotticus (or arytænoidei

obliqui); they act like the foregoing. The action of these muscles is indicated in fig. 435; the arrows point to the line of traction.

Pathological.—Paralysis of this muscle enfeebles the voice and makes it hoarse, as much air escapes between the arytenoid cartilages during phonation.

3. In order that the **vocal cords** be **approximated** to each other, which occurs during phonation, the processus vocales of the arytenoid cartilages must be closely apposed, whereby they must be rotated inwards and downwards. This result is brought about by the processus musculares being moved in a forward and upward direction by the **thyro-arytenoid muscles.** These muscles are applied to, and in fact are embedded in, the substance of the elastic vocal cords, and their fibres reach to the external surface of the arytenoid cartilages. When they contract, they rotate these cartilages so that the processus vocales must rotate inwards. The glottis vocalis is thereby narrowed to a mere slit (fig. 436), whilst the glottis respiratoria remains as a broad triangular opening. The action of these muscles is indicated in fig. 436.

The **lateral crico-arytenoid muscle** is inserted into the anterior margin of the articular surface of the arytenoid cartilage; hence, it can only pull the cartilage forwards; but some have supposed that it can also rotate the arytenoid cartilage in a manner similar to the thyro-arytenoid (?), with this difference, that the processus vocales do not come so close to each other.

Pathological.—Paralysis of both thyro-arytenoid muscles causes loss of voice.

4. The **vocal cords are rendered tense** by their points of attachment being removed from each other by the action of muscles. The chief agents in this action are the **crico-thyroid muscles,** which pull the thyroid cartilage forwards and downwards. At the same time, however, the posterior crico-arytenoids must pull the arytenoid cartilages slightly backwards, and also keep them fixed.

The genio-hyoid and thyro-hyoid, when they contract, pull the thyroid upwards and forwards towards the chin, and also tend to increase the tension of the vocal cords (*C. Mayer, Grützner*). According to Kiesselbach the crico-thyroid elevates the ring of the cricoid cartilage. The plate of the cricoid is thereby directed backwards and downwards, and thus causes tension of the vocal cords.

Pathological.—Paralysis of the crico-thyroid causes the voice to become harsh and deep, owing to the vocal cords not being sufficiently tense.

Position during Phonation.—The tension of the vocal cords brought about in this way is not of itself sufficient for phonation. The triangular aperture of the glottis respiratoria between the arytenoid cartilages, produced by the unaided action of the internal thyro-arytenoid muscles (sec 3) must be closed by the action of the transverse and oblique arytenoid muscles. The vocal cords themselves must have a concave margin, which is obtained through the action of the crico-thyroids and posterior crico-arytenoids, so that the glottis vocalis presents the appearance of a myrtle leaf (*Henle*), while the rima glottidis has the form of a linear slit (fig. 440). The contraction of the internal thyro-arytenoid converts the concave margin of the vocal cords into a straight margin. This muscle adjusts the delicate variations of tension of the vocal cords themselves, causing more especially such variations as are necessary for the production of tones of slightly different pitch. As these muscles come close to the margin of the cords, and are securely woven, as it were, amongst the elastic fibres of which the cords consist, they are specially adapted for the above-mentioned purpose. When the muscles contract, they give the necessary resistance to the cords, thus favouring their vibration. As some of the muscular fibres end in the elastic fibres of the cords, these fibres, when they contract, can render certain parts of the cords more tense than others, and thus favour the modifications in the formation of the tones. The *coarser* variations in the tension of the vocal cords are produced by the separation of the thyroid from the arytenoid cartilages, while the *finer* variations of tension are produced by the thyro-arytenoid muscles.

The value of the elastic-tissue of the cords does not depend so much upon its extensibility as upon its property of shortening without forming folds and creases.

Pathological.—In paralysis of these muscles, the voice can only be produced by forcible expiration, as much air escapes through the glottis; the tones are at the same time deep and impure. Paralysis of the muscle of one side causes flapping of the vocal cord on that side (*Gerhardt*).

5. **The relaxation of the vocal cords** occurs spontaneously when the stretching forces cease to act; the elasticity of the displaced thyroid and arytenoid cartilages comes into play, and restores them to their original position. The vocal cords are also relaxed by the action of the thyro-arytenoid and lateral crico-arytenoid muscles.

It is evident, from the above statements, that **tension of the vocal cords** and **narrowing of the glottis** are necessary for **phonation.** The tension is produced by the crico-thyroids and posterior crico-arytenoids; the narrowing of the glottis respiratoria by the arytenoids, transverse and oblique, the glottis vocalis being narrowed by the thyro-arytenoids and (? lateral crico-arytenoids), the former muscles causing the cords themselves to become tense.

Nerves (§ 352, 5).—The crico-thyroid is supplied by the superior laryngeal branch of the vagus, which at the same time is the sensory nerve of the mucous membrane of the larynx. All the other intrinsic muscles of the larynx are supplied by the inferior laryngeal.

[Section of the superior laryngeal nerve in the horse, although it is a purely sensory nerve in this animal, causes cessation of the movements of the glottis on that side, and subsequently unilateral atrophy of the laryngeal muscles (*Möller*, *Exner*).]

The mucous membrane of the larynx is richly supplied with elastic fibres, and so is the sub-mucosa. The **sub-mucosa** is more lax near the entrance to the glottis and in the ventricle, of Morgagni, which explains the enormous swelling that sometimes occurs in these parts in œdema glottidis. A thin clear limiting membrane lies under the epithelium. The **epithelium** is stratified, cylindrical, and ciliated with intervening goblet cells. On the true vocal cords and the anterior surface of the epiglottis, however, this is replaced by stratified squamous epithelium, which covers the small papillæ of the mucous membrane. Numerous branched **mucous glands** occur over the cartilages of Wrisberg, the cushion of the epiglottis, and in the ventricles of Morgagni; in other situations, as on the posterior surface of the larynx, the glands are more scattered. The **blood-vessels** form a dense capillary plexus under the membrana propria of the mucous membrana; under this, however, there are other two strata of blood-vessels. The **lymphatics** form a superficial narrow meshwork under the blood-capillaries, with a deeper, coarser plexus. The medullated **nerves** have ganglia in their branches, but their mode of termination is unknown. [W. Stirling has described a rich sub-epithelial plexus of medullated nerve-fibres on the anterior surface of the epiglottis, while he finds that there are ganglionic cells in the course of the superior laryngeal nerve.] **Cartilages.**—The thyroid, cricoid, and nearly the whole of the arytenoid cartilages consist of *hyaline* cartilage. The two former are prone to ossify. The apex and processus vocalis of the arytenoid cartilages consist of *yellow fibro-cartilage*, and so do all the other cartilages of the larynx. The larynx grows until about the sixth year, when it rests for a time, but it becomes again much larger at puberty (§ 434).

314. LARYNGOSCOPY.—The Laryngoscope consists of a small mirror fixed to a long handle, at an angle of 125° to 130° (fig. 437, *a*, *b*). When the mouth is opened, and the tongue drawn forward, the mirror is introduced, as is shown in fig. 438. The position of the mirror must be varied, according to the position of the larynx we wish to examine; in some cases the soft palate has to be raised by the back of the mirror, as in the position *b*. A picture of the part of the larynx examined is formed in the small mirror, the rays of light passing in the direction indicated by the dotted lines from the mirror; they are reflected at the same angle through the mouth into the eye of the observer, who must place himself in the direction of the reflected rays.

The illumination of the larynx is accomplished either by means of direct sunlight or by light from an artificial source, *e.g.*, an ordinary lamp, an oxyhydrogen lime-light, or the electric light. The beam of light impinges upon a *concave mirror* of 15 to 20 centimetres focus, and 10 centimetres in width, and from its surface the concentrated beam of light is reflected through the mouth of the patient, and directed upon the small mirror held in the back part of the throat.

The beam of light is reflected at the same angle toward the larynx by the small throat mirror, so that the larynx is brightly illuminated. The observer has now to direct his eye in the same direction as the illuminating rays, which can be accomplished by having a hole in the centre of the concave mirror, through which the observer looks. Practically, however, this is unnecessary; all that is necessary is to fix the concave mirror to the forehead by means of a broad elastic band, so that the observer, by looking just under the margin of the concave mirror, can see the picture of the larynx in the small throat mirror (fig. 438).

In order to examine the larynx, place the patient immediately in front of you, and cause him to open his mouth and protrude his tongue. A lamp is placed at the side of the head of the

Fig. 437.

Vertical section through the head and neck, to the 1st dorsal vertebra, *a*, position of the laryngoscope on observing the posterior part of the glottis, arytenoid cartilages, and upper surface of the posterior wall of the larynx; *b*, its position on observing the anterior angle of the glottis. Large, *a*, and *b*, small laryngoscopic mirrors.

patient, and light from this source is reflected from the concave mirror on the observer's forehead, and concentrated upon the laryngoscopic mirror introduced into the back part of the throat of the patient (fig. 438).

Oertel was able, by means of a rapid intermittent illumination of the larynx through a stroboscopic disc, to study the movements of the vocal cords directly with the eye. Simanowsky put a photographic camera in the position of the eye, and photographed the movements of the vocal cords of an artificial larynx. [Brown and Behnke have photographed the human vocal cords.]

Historical.—After Bozzini (1807) gave the first impulse towards the investigation of the internal cavities of the body, by illuminating them with the aid of mirrors, Babington (1829) actually observed the glottis in this way. The famous singer, Manuel Garcia (1854), made

investigations both on himself and other singers, regarding the movements of the vocal cords, during respiration and phonation. The examination of the larynx by means of the laryngoscope was rendered practicable chiefly by Türck (1857) and Czermak, the latter observer being the first to use the light of a lamp for the illumination of the larynx. Rhinoscopy was actually first practised by Baumès (1838), but Czermak was the first person who investigated this subject systematically.

Laryngeal Electrodes.—V. Ziemssen introduces long narrow electrodes into the larynx, to stimulate the muscles and study their actions. Rossbach finds that the muscles and nerves of the interior of the larynx may be stimulated by stimulating the skin, *i.e.*, percutaneously. These methods are used both for physiological and therapeutical purposes.

Fig. 438.
Method of examining the larynx.

Picture of the Larynx.—Fig. 439 shows the following structures:—*L.*, the root of the tongue, with the ligamentum glosso-epiglotticum continued from its middle: on each side of the latter are *V. V.*, the so-called *valleculæ.* The *epiglottis* (*E.*) appears like an arched upper lip; under it, during normal respiration, is the lancet-shaped *glottis* (*R.*) and on each side of it the *true vocal cords* (*L.v*). The length of the vocal cord in a child is 6 to 8 mm., in the female 10 to 15 mm. when they are relaxed, and 15 to 20 mm. when tense. In man, the lengths under the same conditions are 15 to 20 mm. and 20 to 25 mm. The breadth varies from 2 to 5 mm. On the external side of each vocal cord is the entrance to the *sinus of Morgagni* (*S.M.*), represented as a dark line. Further upwards and more external are (*L.v.s.*) the upper or *false vocal cords.* [The upper or false vocal cords are red, the lower or true, white.] On each side of *P.* are (*S.S.*) the apices of the *cartilages of Santorini*, placed upon the apices of the arytenoid cartilages, while immediately behind is the wall of the pharynx, *P.* In the aryteno-epiglottidean fold are (*W. W.*) the *cartilages of Wrisberg*, while outside these are the depressions (*S.p.*) constituting the *sinus piriformes.*

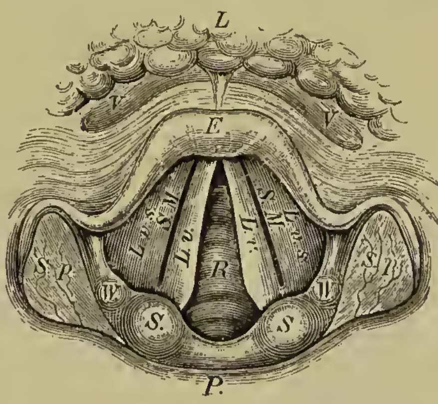


Fig. 439.
The larynx, as seen with the laryngoscope. *L.*, tongue; *E.*, epiglottis; *V.*, vallecula; *R.*, glottis; *L.v.*, true vocal cords; *S.M.*, sinus Morgagni; *L.v.s.*, false vocal cords; *P.*, position of pharynx; *S.*, cartilage of Santorini; *W.*, of Wrisberg; *S.p.*, sinus piriformes.

During normal respiration the glottis has the form of a lancet-shaped slit between the bright yellowish-white vocal cords (fig. 440). If a **deep inspiration** be taken, the glottis is considerably widened (fig. 441), and if the mirror be favour-

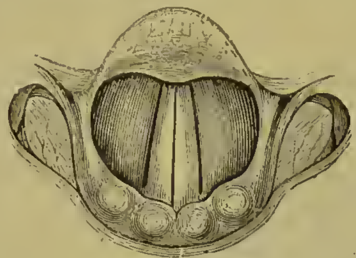


Fig. 440.
Position of the vocal cords on uttering a high note.

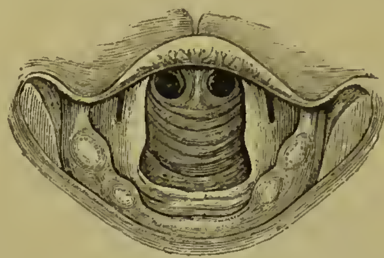


Fig. 441.
View of the rings and bifurcation of trachea.

ably adjusted we may see the rings of the trachea, and even the bifurcation of the trachea.

If a **high note** be uttered, the glottis is contracted to a very narrow slit (fig. 440).

Rhinoscopy.—If a small mirror, fixed to a handle at an angle of 100° to 110°, be introduced into the pharynx, as shown in fig. 442, and if the mirror be directed *upwards*, certain structures are with difficulty rendered visible (fig. 443). In the middle is the septum narium (*S.n.*), and on each side of it the long oval large posterior nares (*Ch.*), below this the *soft palate* (*P.m*), with the pendant *uvula* (*U.*). In the posterior nares are the posterior extremities of the lower (*C.i.*), middle (*C.m.*), and upper *turbinated bones* (*C.s.*). At the upper part, a portion of the roof of the pharynx (*O.R.*) is seen, with the arched masses of adenoid tissue lying between the openings of the *Eustachian tubes* (*T.T.*), and called by Luschka the *pharyngeal tonsils.* External to the openings of the Eustachian tube is the *tubular eminence* (*W.*), and outside this is the groove of Rosenmüller (*R.*).

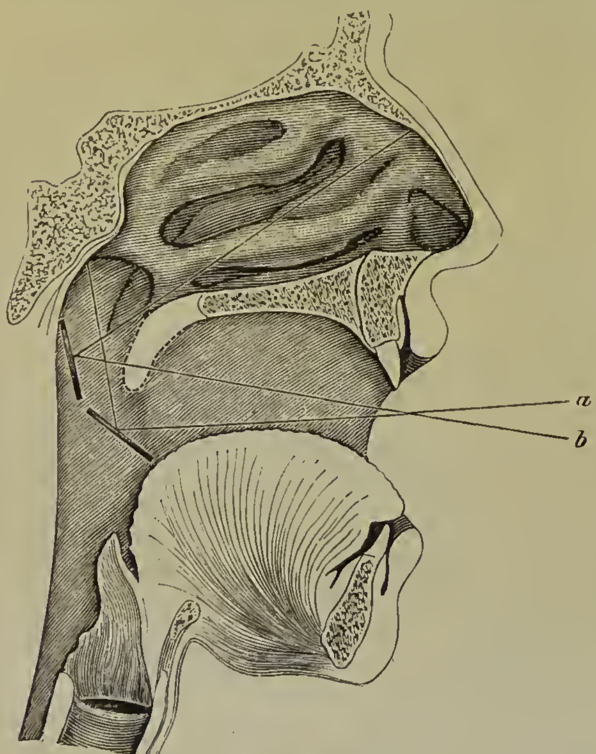


Fig. 442.
Position of the laryngoscopic mirror in rhinoscopy.

Experiments on the Excised Larynx.—Ferrein (§ 741) and Joh. Müller made experiments upon the excised larynx. A tracheal tube was tied into the excised human larynx, and air was blown through it, the pressure being measured by means of a mercurial manometer, while various arrangements were adopted for putting the vocal cords on the stretch and for opening or closing the glottis.

315. CONDITIONS INFLUENCING THE LARYNGEAL SOUNDS.—The **pitch of the note** emitted by the larynx depends upon :—

1. **The Tension of the Vocal Cords,** *i.e.*, upon the degree of contraction of the crico-thyroid and posterior crico-arytenoid muscles, and also of the internal thyro-arytenoids (§ 313, II., 4).

2. **The Length of the Vocal Cords.**—(*a*) Children and females with short

vocal cords produce high notes. (*b*) If the arytenoid cartilages are pressed together by the action of the arytenoid muscles (transverse and oblique), so that the vocal cords alone can vibrate, while their intercartilaginous portions lying between the processus vocales do not, the tone thereby produced is higher (*Garcia*). In the production of low notes, the vocal cords, as well as the margins of the arytenoid cartilages, vibrate. At the same time the space above the entrance to the glottis is enlarged and the larynx becomes more prominent. (*c*) Every individual has a certain medium pitch of his voice, which corresponds to the smallest possible tension of the intrinsic muscles of the larynx.

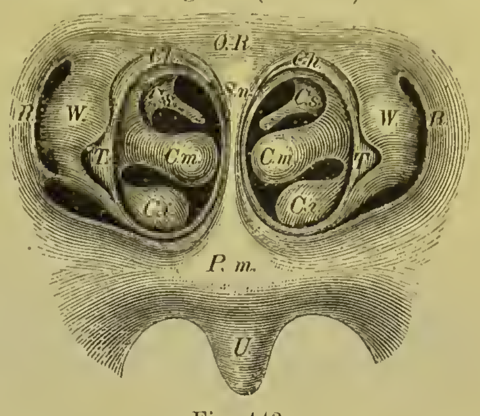


Fig. 443.
Composite rhinoscopic view. *S.n.*, Septum narium ; *C.i.*, *C.m.*, *C.s.*, lower, middle, and upper turbinated bones ; *T.*, Eustachian tube ; *W.*, tubular eminence ; *R.*, groove of Rosenmüller ; *P.m.*, soft palate ; *O.R.*, roof of pharynx ; *U.*, uvula.

3. **The Strength of the Blast.**—That the strength of the blast from below raises the pitch of the tones of the human larynx is shown by the fact, that tones of the highest pitch can only be uttered by powerful expiratory efforts. With tones of *medium* pitch, the pressure of the air in the trachea is 160 mm., with *high* pitch 200 mm., and with *very high* notes 945 mm., and in *whispering* 20 mm., of water (*Cagniard-Latour*). These results were obtained in a case of tracheal fistula.

Accessory Phenomena.—The following as yet but partially explained phenomena are observed in connection with the production of high notes :—(*a*) As the pitch of the note rises, the larynx is elevated, partly because the muscles raising it are active, partly because the increased intratracheal pressure so lengthens the trachea, that the larynx is thereby raised ; the uvula is raised more and more (*Labus*). (*b*) The upper vocal cords approximate to each other more and more, without, however, coming into contact, or participating in the vibrations. (*c*) The epiglottis inclines more and more backwards over the glottis.

4. **The falsetto voice**, with its soft timbre and the absence of resonance or pectoral fremitus in the air-tubes, is particularly interesting. Oertel observed that, during the falsetto voice, the vocal cords vibrated so as to form nodes across them, but sometimes there was only one node, so that the free margin of the cord and the basal margin vibrated, being separated from each other by a nodal line (parallel to the margins of the vocal cord). During a high falsetto note there may be three such nodal lines parallel to each other. The nodal lines are produced probably by a partial contraction of the fibres of the thyro-arytenoid muscle (p. 636), while at the same time the vocal cords must be reduced to as thin plates as possible by the action of the crico-thyroid, posterior arytenoid, thyro- and genio-hyoid muscles (*Oertel*). The form of the glottis is elliptical, while with the chest-voice the vocal cords are limited by straight surfaces ; the air also passes more freely through the larynx.

Oertel also found that during the **falsetto voice** the epiglottis is erect. The apices of the arytenoid cartilages are slightly inclined backwards, the whole larynx is larger from before backwards, and narrower from side to side, the aryepiglottidean folds are tense with sharp margins, and the entrance to the ventricles of Morgagni is narrowed. The vocal cords are narrower, the processus vocales touch each other. The rotation of the arytenoid cartilages necessary for this is brought about by the action of the crico-arytenoid alone, while the thyro-arytenoid is to be regarded only as an accessory aid. The pitch of the note is increased solely by increased tension of the vocal cords. In addition, there are a number of transverse and longitudinal *partial vibrations*. During the **chest-voice**, a smaller part of the margin vibrates than in the falsetto voice, so that in the production of the latter we are conscious of less muscular exertion in the larynx. The uvula is raised to the horizontal position.

Production of Voice.—In order that voice be produced, the following conditions

are necessary :—(1) The necessary amount of air is collected in the chest; (2) the larynx and its parts are fixed in the proper position ; (3) air is then forced by an expiratory effort either through the linear chink of the closed glottis, so that the latter is forced open, or at first some air is allowed to pass through the glottis without producing a sound, but as the blast of air is strengthened the vocal cords are thrown into vibration.

316. RANGE OF THE VOICE.—The range of the human voice for chest notes is given in the following scheme :—

The accompanying figures indicate the number of vibrations per second in the corresponding tone. It is evident that from *c'* to *f'* is common to all voices, nevertheless, they have a different timbre. The lowest note or tone, which, however, is only occasionally sung by bass singers, is the contra-F, with 42 vibrations—the highest note of the soprano voice is *a'''*, with 1708 vibrations.

Timbre.—The voice of every individual has a peculiar *quality*, *clang*, or *timbre*, which depends upon the shape of all the cavities connected with the larynx. In the production of *nasal tones*, the air in the nose is caused to vibrate strongly, so that the entrance to the nares must necessarily be open.

317. SPEECH—THE VOWELS.—The motor processes connected with the production of **speech** occur in the **resonating cavities**, the pharynx, mouth, and nose, and are directed towards the production of musical tones and noises.

Whispering and Audible Speech.—When sounds or noises are produced in the resonating chambers, the larynx being passive, the vox clandestina, or **whispering** is produced ; when the vocal cords, however, vibrate at the same time, "**audible speech**" is produced. [Whispering, therefore, is speech without voice.] Whispering may be fairly loud, but it requires great exertion, *i.e.*, a great expiratory blast, for its production ; hence it is very fatiguing. It may be performed both with inspiration and expiration, while audible speech is but temporary and indistinct, if it is produced during inspiration. Whispering is caused by the sound produced by the air passing over the obtuse margins of the cords. During the production of *audible sounds*, however, the sharp margins of the vocal cords are directed towards the air by the position of the processus vocales.

During speech the **soft palate** is in action ; at each word it is raised, while at the same time, Passavant's transverse band is formed in the pharynx (§ 156). The soft palate is raised highest when **u** and **i** are sounded, then with *o* and *e*, and least with *a*. When sounding **m** and **n** it does not move ; it is high (like **n**) during the utterance of the explosives. With **l**, **s**, and especially with the guttural **r**, it exhibits a trembling movement (*Gentzen*, *Falkson*).

Speech is composed of **vowels** and **consonants**.

A. Vowels (analysis and artificial formation, § 413).—**A.** During **whispering**, a vowel is the musical tone produced, either during expiration or inspiration, by the inflated characteristic form of the mouth, which not only has a definite *pitch*, but also a particular and characteristic *timbre*. The characteristic form of the mouth may be called "*vowel cavity*."

I. The pitch of the vowels may be estimated musically. It is remarkable that the fundamental tone of the "vowel-cavity" is nearly constant at different ages and in the sexes. The different capacities of the mouth can be compensated for by different sizes of the oral aperture. The pitch of the vowel-cavity may be estimated by placing a number of vibrating tuning-forks of different pitch in front of the mouth, and testing them until we find the one which corresponds with the fundamental tone of the vowel-cavity. This is known by the fact, that the tone of the tuning-fork is intensified by the *resonance* of the air in the mouth, or the vibrations may be transferred to a vibrating membrane and recorded on a smoked surface, as in the phonautograph of Donders.

According to König, the **fundamental tones** of the vowel-cavity are for

$$U = b,\ O = b'\ A = b'',\ E = b''',\ I = b''''.$$

If the vowels be whispered in this series, we find at once that their pitch rises. The fundamental tone in the production of a vowel may vary within certain limits. This may be shown by giving the mouth the characteristic position and then percussing the cheeks (*Auerbach*); the sound emitted is that of the vowel, whose pitch will vary accordingly to the position of the mouth.

When **sounding A**, the mouth has the form of a funnel widening in front (fig. 444, A). The tongue lies in the floor of the mouth, and the lips are wide open. The soft palate is moderately raised (*Czermak*). It is more elevated successively with O, E, U, I. The hyoid bone appears as if at rest, but the larynx is slightly raised. It is higher than with U, but lower than with I.

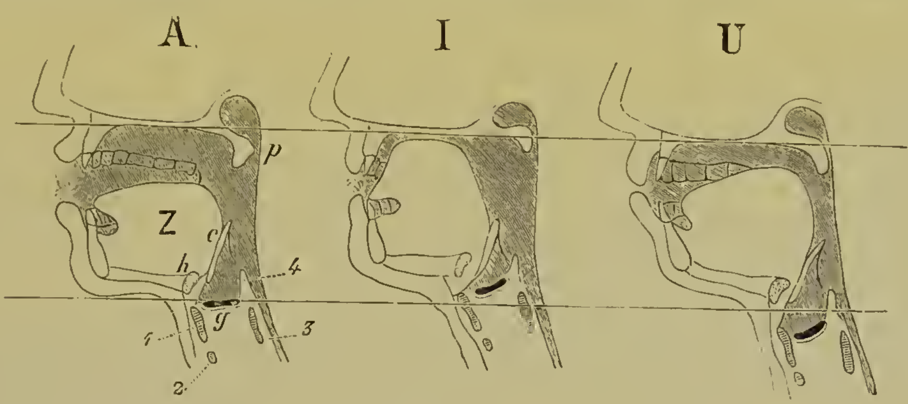


Fig. 444.

Section of the parts concerned in phonation. Z, tongue ; *p*, soft palate ; *c*, epiglottis ; *g*, glottis ; *h*, hyoid bone ; 1, thyroid, 2, 3 cricoid, 4, arytenoid cartilage.

If we sound A to I, the larynx and the hyoid bone retain their *relative* position, but both are raised. In passing from A to U, the larynx is depressed as far as possible. The hyoid bone passes slightly forward (*Brücke*). When sounding A, the space between the larynx, posterior wall of the pharynx, soft palate, and the root of the tongue, is only moderately wide; it becomes wider with E, and especially with I (*Purkinje*), but it is smallest with U.

When **sounding U** (fig. 444), the form of the cavity of the mouth is like that of a capacious flask with a short, narrow neck. The whole resonance apparatus is then longest. The lips are protruded as far as possible, are arranged in folds and closed, leaving only a small opening. The larynx is depressed as far as possible, while the root of the tongue is approximated to the posterior margin of the palatine arch.

When **sounding O**, the mouth, as in U, is like a wide-bellied flask with a short neck, but the latter is shorter and wider as the lips are nearer to the teeth. The larynx is slightly higher than with U, while the resonance chambers also are shorter (fig. 444).

When **sounding I**, the cavity of the mouth, at the posterior part, is in the form of a small-bellied flask with a long narrow neck, of which the belly has the fundamental tone, f, the neck that of d'''. The resonating chambers are shortest, as the larynx is raised as much as possible, while the mouth, owing to the retraction of the lips, is bounded in front by the teeth. The cavity between the hard palate and the back of the tongue is exceedingly narrow, there being only a median narrow slit. Hence, the air can only enter with a clear piping noise, which sets even the vertex of the skull in vibration, and when the ears are stopped the sounds seem very shrill. When the larynx is depressed and the lips protruded, as for sounding U, I cannot be sounded.

When sounding E, which stands next to I, the cavity has also the form of a flask with a small belly (fundamental tone f′), and with a long, narrow neck (fundamental tone, b‴.) The neck is wider, so that it does not give rise to a piping noise. The larynx is slightly lower than for I, but not so high as for A.

Fundamentally, there are only *three primary* vowels—I, A, U, the others and the so-called diphthongs standing between them (*Brücke*).

Diphthongs occur when, *during vocalisation*, we pass from the position of one vowel into that of another. Distinct diphthongs are sounded only on passing from one vowel with the mouth wide open to one with the mouth narrow; during the converse process, the vowels appear to our ear to be separate (*Brücke*).

II. Timbre or **Clang-Tint.**—Besides its pitch, every vowel has a special timbre, quality, or clang-tint.

The vocal timbre of U (whispering) has, in addition to its fundamental tone, b, a deep piping timbre. The timbre depends upon the number and pitch of the *partials* or *overtones* of the vowel sound (§ 415).

Nasal Timbre.—The timbre is modified in a special manner when the vowels are spoken with a "nasal" twang, which is largely the case in the French language. The nasal timbre is produced by the soft palate not cutting off the nasal cavity completely, which happens every time a *pure* vowel is sounded, so that the air in the nasal cavity is thrown into sympathetic vibration. When a vowel is spoken with a nasal timbre, air passes out of the nose and mouth simultaneously, while, with a pure vowel sound, it passes out only through the mouth.

When sounding a pure vowel (non-nasal), the shutting off of the nasal cavity from the mouth is so complete, that it requires an artificial pressure of 30 to 100 mm. of mercury to overcome it (*Hartmann*).

The vowels, a, ä (æ), ö, (œ) o, e, are used with a nasal timbre—a nasal i does not occur in any language. Certainly it is very difficult to sound it thus, because when sounding i the mouth is so narrow that when the passage to the nose is open, the air passes almost completely through the latter, whilst the small amount passing through the mouth scarcely suffices to produce a sound.

In sounding vowels, we must observe if they are sounded through a previously closed glottis, as is done in the German language in all words beginning with a vowel (spiritus lenis). The glottis, however, may be previously opened with a preliminary breath, followed by the vowel sound; we obtain the aspirate vowel (spiritus asper of the Greeks).

B. If the vowels are sounded in an **audible** tone, *i.e.*, along with the sound from the larynx, the fundamental tone of the vocal cavity strengthens in a characteristic manner the corresponding partial tones present in the laryngeal sound (*Wheatstone*, *v. Helmholtz*).

318. CONSONANTS.—The consonants are **noises** which are produced at certain parts of the resonance chamber. [As their name denotes, they can only be sounded in conjunction with a vowel.]

Classification.—The most obvious classification is according to—(I.) Their *acoustic properties*, so that they are divided into—(1) *liquid* consonants, *i.e.*, such as are appreciable without a vowel (m, n, l, r, s); (2) *mutes*, including all the others, which cannot be distinctly heard without an accompanying vowel. (II.) According to their *mechanism of formation*, as well as the type of the organ of speech, by which they are produced. They are divided into—

1. **Explosives.**—Their enunciation is accompanied by a kind of bursting open of an obstacle, or an explosion, occasioned by the confined and compressed air which causes a stronger or weaker noise; or, conversely, the current of air is suddenly *interrupted*, while, at the same time, the nasal cavities are cut off by the soft palate.

2. **Aspirates**, in which one part of the canal is constricted or stopped, so that the air rushes out through the constriction, causing a faint whistling noise. (The nasal cavity is cut off.) In uttering L, which is closely related to the aspirates, but differs from them in that the narrow passage for the rush of air is not in the middle, but at both sides of the middle of the closed part. (The nasal cavity is shut off.)

3. **Vibratives**, which are produced by air being forced through a narrow portion of the canal, so that the margins of the narrow tube are set in vibration. (The nasal cavity is shut off.)

4. **Resonants** (also called nasals or semi-vowels). The nasal cavity is completely free, while the vocal canal is completely closed in the front part of the oral channel. According to the position of the obstruction in the oral cavity, the air in a larger or smaller portion of the mouth is thrown into sympathetic vibration.

We may also classify them according to the *position* in *which they are produced* —the "**articulation positions**" of Brücke. These are:—

A. Between both lips; B, between the tongue and the hard palate; C, between the tongue and the soft palate; D, between the true vocal cords.

A. Consonants of the First Articulation Position.

1. **Explosive Labials.**—b, the voice is sounded before the slight explosion occurs; p, the voice is sounded after the much stronger explosion has taken place (*Kempelen*). [The former is spoken of as "voiced" and the latter as "breathed."]

2. **Aspirate Labials.**—f, between the upper incisor teeth and the lower lip (labiodental). It is absent in all true Slavic words (*Purkiñe*); v, between both lips (labial); **w** is formed when the mouth is in the position for f, but instead of merely forcing in the air, the voice is sounded at the same time. Really there are two different w—one corresponding to the **labial f**, as in würde, and the labiodental, *e.g.*, quelle (*Brücke*).

3. **Vibrative Labials.**—The burring sound, emitted by grooms, but not used in civilised language.

4. **Resonant Labials.**—**m** is formed essentially by sounding the voice whereby the air in the mouth and nose is thrown into sympathetic vibration ["voiced"].

B. Consonants of the Second Articulation Position.

1. The **explosives**, when enunciated sharply and without the voice, are **T** hard (also **dt** and **th**); when they are feeble and produced along with simultaneous laryngeal sounds (voice), we have **D** soft.

2. The **aspirates** embrace **S**, including **s** sharp, written **s s** or **s z**, which is produced without any audible laryngeal vibration; or soft, which requires the voice. Then, also, there are modifications according to the position where the noises are produced. The sharp aspirates include **Sch**, and the hard English **Th**; to the soft belong the French **J** soft, and the English **Th** soft. **L**, which occurs in many modifications, appears here, *e.g.*, the **L** soft of the French. **L** may be sounded soft with the voice, or sharp without it.

3. The **vibrative**, or **R**, which is generally voiced, but it can be formed without the larynx. The **resonants** are **N**-sounds, which also occur in several modifications.

C. Consonants of the Third Articulation Position.

1. The **explosives** are the **K**-sounds, which are hard and breathed and not voiced; **G**-sounds, which are voiced.

2. The **aspirates**, when hard and breathed but not voiced, the **Ch**, and when sounded softly and not voiced, **J** is formed.

3. The **vibrative** is the palatal **R**, which is produced by vibration of the uvula (*Brücke*).

4. The **resonant** is the palatal **N**.

D. Consonants of the Fourth Articulation Position.

1. An **explosive** sound does not occur when the glottis is forced open, if a vowel is loudly sounded with the glottis previously closed. If this occurs during whispering, a feeble short noise, due to the sudden opening of the glottis, may be heard.

2. The **aspirates** of the glottis are the **H**-sounds, which are produced when the glottis is moderately wide.

3. A **glottis-vibrative** occurs in the so-called laryngeal **R** of lower Saxon (*Brücke*).

4. A **laryngeal resonant** cannot exist.

The **combination** of different consonants is accomplished by the successive movements necessary for each being rapidly executed. Compound consonants, however, are such as are formed when the oral parts are adjusted simultaneously for two different consonants, so that a mixed sound is formed from two. Examples: **Sch—tsch, tz, ts—Ps** (ψ)—**Ks** (XΞ).

319. **PATHOLOGICAL VARIATIONS OF VOICE AND SPEECH.—Aphonia.**—Paralysis of the motor nerves (vagus) of the larynx by injury, or the pressure of tumours, causes **aphonia** or **loss of voice** (*Galen*). In aneurism of the aortic arch, the left recurrent nerve may be paralysed from pressure. The laryngeal nerves may be temporarily paralysed by rheumatism, over-exertion and hysteria, or by serous effusions into the laryngeal muscles. If the tensors are paralysed, **monotonia** is the chief result; the disturbances of respiration in paralysis of the larynx are important. As long as the respiration is tranquil, there may be no disturbance, but as soon as increased respiration occurs, great dyspnœa sets in, owing to the inability of the glottis to dilate.

If only **one vocal cord** is paralysed, the voice becomes impure and falsetto-like, while we may feel from without that there is less vibration on the paralysed side (*Gerhardt*). Sometimes

the vocal cords are only so far paralysed that they do not move during phonation, but do so during forced respiration and during coughing (**phonetic paralysis**).

Diphthongia.—Incomplete unilateral paralysis of the recurrent nerve is sometimes followed by a **double tone**, owing to the unequal tension of the two vocal cords. According to Türck and Schnitzler, however, the double tone occurs when the two vocal cords touch at some part of their course (*e.g.*, from the presence of a tumour, fig. 445), so that the glottis is divided into two unequal portions, each of which produces its own sound.

Hoarseness is caused by mucus upon the vocal cords, by roughness, swelling, or laxness of the cords. If, while speaking, the cords are approximated, and suddenly touch each other, the "speech is broken," owing to the formation of nodal points (§ 352). Disease of the pharynx, naso-pharyngeal cavity, and uvula may produce a change in the voice *reflexly*.

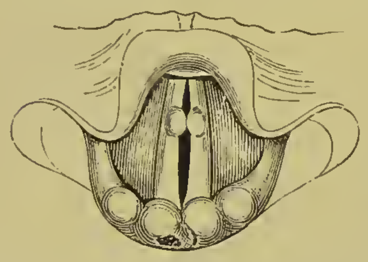


Fig. 445.

Tumours on the vocal cords causing double tone from the larynx.

Paralysis of the soft palate (as well as congenital perforation or cleft palate) causes a *nasal timbre* of all vowels; the former renders difficult the normal formation of consonants of the third articulation position; resonance is imperfect, while the explosives are weak, owing to the escape of the air through the nose.

Paralysis of the tongue weakens I; E and A (Æ) are less easily pronounced, while the formation of consonants of the second and third articulation position is affected. The term **aphthongia** is applied to a condition in which every attempt to speak is followed by spasmodic movements of the tongue (*Fleury*).

In **paralysis of the lips** (*facial nerve*), and in hare-lip, regard must be had to the formation of consonants of the first articulation position. When the nose is closed, the speech has a characteristic sound. The normal formation of resonants is of course at an end. After excision of the larynx, a metal reed, enclosed in a tube, and acting like an artificial larynx, is introduced between the trachea and the cavity of the mouth (*Czerny*).

Stammering is a disturbance of the formation of sounds. [Stammering is due to long-continued spasmodic contraction of the diaphragm, just as hiccough is (§ 120), and, therefore, it is essentially a spasmodic inspiration. As speech depends upon the expiratory blast, the spasm prevents expiration. It may be brought about by mental excitement or emotional conditions. Hence, the treatment of stammering is to regulate the respirations. In **stuttering**, which is defective speech due to inability to form the proper sounds, the breathing is normal.]

320. COMPARATIVE—HISTORICAL.—**Speech** may be classified with the "**expression of the emotions**" (*Darwin*). Psychical excitement causes in man characteristic movements, in which certain groups of muscles are always concerned, *e.g.*, laughing, weeping, the facial expression in anger, pain, shame, &c. These movements afford a means whereby one creature can communicate with another. Primarily in their origin, the movements of expression are *reflex* motor phenomena; when they are produced for purposes of explanation, they are voluntary imitations of this reflex. Besides the emotional movements, impressions upon the sense-organs produce characteristic reflex movements, which may be used for purposes of expression (*Geiger*), *e.g.*, stroking or painful stimulation of the skin, movements after smelling pleasant or unpleasant or disagreeable odours, the action of sound and light, and the perception of all kinds of objects.

The expression of the emotions occurs in its simplest form in what is known as expression by means of **signs** or pantomime or **mimicry**. Another means is the **imitation of sounds** by the organ of speech, constituting *onomatopoesy*, *e.g.*, the hissing of a stream, the roll of thunder, the tumult of a storm, whistling, &c. The expression of speech is, of course, dependent upon the process of ideation and perception.

The *occurrence of different sounds* in different languages is very interesting. Some languages (*e.g.*, of the Hurons) have no labials; in some South Sea Islands no laryngeal sounds are spoken; *f* is absent in Sanscrit and Finnish; the short *c*, *o*, and the soft sibilants in Sanscrit; *d*, in Chinese and Mexican; *s*, in many Polynesian languages; *r*, in Chinese, &c.

Voice in Animals.—Animals, more especially the higher forms, can express their emotions by facial and other gestures. The vocal organs of **mammals** are essentially the same as those of man. Special *resonance organs* occur in the orang-outang, mandril, macacus, and mycetes monkeys, in the form of large cheek pouches, which can be inflated with air, and open between the larynx and the hyoid bone.

Birds have an upper (**larynx**) and a lower larynx (**syrinx**); the latter is placed at the bifurcation of the trachea, and is the true vocal organ. Two folds of mucous membrane (three in singing birds) project into each bronchus, and are rendered tense by muscles, and are thus adapted to serve for the production of voice.

Amongst **reptiles**, the tortoises produce merely a sniffing sound, which in the Emys has a peculiar piping character. The blind snakes are voiceless, the chameleon and the lizards have a very feeble voice; the cayman and crocodile emit a feeble roaring sound, which is lost in

some adults owing to changes in the larynx. The *snakes* have no special vocal organs, but by forcing out air from their capacious lung, they make a peculiar hissing sound, which in some species is loud. Amongst **amphibians**, the frog has a larynx provided with muscles. The sound emitted without any muscular action is a deep intermittent tone, while more forcible expiration, with contraction of the laryngeal constrictors, causes a clearer continuous sound. The male, in Rana esculenta, has at each side of the angle of the mouth a sound-bag, which can be inflated with air and acts as a resonance chamber. The "croaking" of the male frog is quite characteristic. In Pipa, the larynx is provided with two cartilaginous rods, which are thrown into vibration by the blast of air, and act like vibrating rods or the limbs of a tuning-fork. Some **fishes** emit sounds, either by rubbing together the upper and lower pharyngeal bones, or by the expulsion of air from the swimming bladder, mouth, or anus.

Some **insects** cause sounds partly by forcing the expired air through their stigmata provided with muscular reeds, which are thus thrown into vibration (bees and many diptera). The wings, owing to the rapid contraction of their muscles, may also cause sounds (flies, cockroach, bees). The Sphinx atropos (death-head moth) forces air from its sucking stomach. In others, sounds are produced by rubbing their legs on the wing-cases (Acridium), or the wing-cases on each other (Gryllus, locust), or on the thorax (Cerambyx), on the leg (Geotrupes), on the abdomen or the margin of the wing (Necrophorus). In Cicadaciæ, membranes are pulled upon by muscles, and are thus caused to vibrate. Friction sounds are produced between the cephalo-thorax and the abdomen in some spiders (Theridium), and in some crabs (Palinurus). Some mollusca (Pecten) emit a sound on separating their shells.

Historical.—The Hippocratic School was aware of the fact that division of the trachea abolished the voice, and that the epiglottis prevented the entrance of food into the larynx. Aristotle made numerous observations on the voice of animals. The true cause of the voice escaped him as well as Galen. Galen observed complete loss of voice after double pneumo-thorax, after section of the intercostal muscles or their nerves, as well as after destruction of part of the spinal cord, even although the diaphragm still contracted. He gave the cartilages of the larynx the names that still distinguish them; he knew some of the laryngeal muscles, and asserted that voice was produced only when the glottis was narrowed. He compared the larynx to a flute. The weakening of the voice, in feeble conditions, especially after loss of blood, was known to the ancients. Dodart (1700) was the first to explain voice as due to the vibration of the vocal cords by the air passing between them.

The production of vocal sounds attracted much attention amongst the ancient Asiatics and Arabians—less amongst the Greeks. Pietro Ponce († 1584) was the first to advocate instruction in the art of speaking in cases of dumbness. Bacon (1638) studied the shape of the mouth for the pronunciation of the various sounds. Kratzenstein (1781) made an artificial apparatus for the production of vowel sounds, by placing resonators of various forms over vibrating reeds. Von Kempelen (1769 to 1791) constructed the first speaking-machine. Rob. Willis (1828) found that an elastic vibrating spring gives the vowels in the series—U, O, A, E, I—according to the depth or height of its tone; further, that by lengthening or shortening an artificial resonator on an artificial vocal apparatus, the vowels may be obtained in the same series. The newest and most important investigations on speech are by Wheatstone, v. Helmholtz, Donders, Brücke, &c., and are mentioned in the context. Hensen succeeded in showing exactly the pitch of vocal tone, thus:—The tone is sung against a König's capsule with a gas flame. Opposite the flame is placed a tuning-fork vibrating horizontally, and in front of one of its limbs is a mirror, in which the image of the flame is reflected. When the vocal tone is of the same number of vibrations as the tuning-fork, the flame in the mirror shows one elevation, if double, *i.e.*, the octave, 2, and with the double octave, 4 elevations.

General Physiology of the Nerves and Electro-Physiology.

321. **STRUCTURE OF THE NERVE ELEMENTS.**—The nervous elements present two distinct forms:—

I. Nerve-Fibres. { Non-medullated. Medullated.   **II. Nerve-Cells.** { Of various forms and functions.

An aggregation of nerve-cells constitutes a **nerve-ganglion.** The **fibres** represent a **conducting apparatus,** and serve to place the central nervous organs in connection with peripheral end-organs. The **nerve-cells,** however, besides transmitting impulses, act as **physiological centres** for automatic or reflex movements, and also for the sensory, perceptive, trophic, and secretory functions.

1. (1) **The non-medullated nerve-fibres** occur chiefly in the sympathetic nervous system, although they are not confined to it; hence they are sometimes called sympathetic nerve-fibres. They occur in several forms:—

1. **Primitive Fibrils.**—The simplest form of nerve-fibre, which is visible with a magnifying power of 500 to 800 diameters linear, consists of **primitive nerve-fibrils.** They are very delicate fibres (fig. 446, 1), often with small varicose swellings here and there in their course, which, however, are due to changes *post-mortem.* They are stained of a brown or purplish colour by the gold-chloride method, and they occur when a nerve-fibre is near its termination, being formed by the splitting up of the axis-cylinder of the nerve-fibre, *e.g.*, in the terminations of the corneal nerves, the optic nerve-layer in the retina, the terminations of the olfactory fibres, and in a plexiform arrangement in non-striped muscle (p. 572). Similar fine fibrils occur in the grey matter of the brain and spinal cord, and in the finely divided processes of nerve-cells.

2. **Naked or simple axial cylinders** (fig. 446, 2), which represent bundles of primitive fibrils held together by a slightly granular cement, so that they exhibit very delicate longitudinal striation with fine granules scattered in their course. The best example is the axial cylinder process of nerve-cells (fig. 446, I, *z*). [The thickness of the axis-cylinder depends upon the number of fibrils entering into its composition.]

3. **Axis-cylinders surrounded with Schwann's sheath,** or **Remak's fibres** (3·8 to 6·8 μ broad), the latter name being given to them from their discoverer (fig. 446, 3). [These fibres are also called **pale** or **non-medullated,** and from their abundance in the sympathetic nervous system, **sympathetic.**] They consist of a sheath, corresponding to Schwann's sheath [neurilemma, or primitive sheath, which encloses an axial cylinder; while lying here and there under the sheath, and between it and the axial cylinder are nerve-corpuscles. These fibres are always fibrillated longitudinally.] The **sheath** is delicate, structureless, and elastic. Dilute acids clear the fibres without causing them to swell up, while gold chloride

makes them brownish-red. They are widely distributed in the sympathetic nerves [*e.g.*, splenic], and in the branches of the olfactory nerves. All nerves in the *embryo*, as well as the nerves of many invertebrata, are of this kind. [According to Ranvier, these fibres do not possess a sheath, but the nuclei are merely applied to the surface, or slightly embedded in the superficial parts of the fibre, so that

Fig. 446.

1, Primitive fibrillæ; 2, axis-cylinder; 3, Remak's fibres; 4, medullated varicose fibre; 5, 6, medullated fibre, with Schwann's sheath; *c*, neurilemma; *t*, *t*, Ranvier's nodes; *b*, white substance of Schwann; *d*, cells of the endoneurium; *a*, axis-cylinder; *x*, myelin drops; 7, transverse section of nerve-fibres; 8, nerve-fibre acted on with silver nitrate and showing Frommann's lines. I, multipolar nerve-cell from the spinal cord; *z*, axial cylinder process; *y*, protoplasmic processes — to the right of it a bipolar cell. II, peripheral ganglionic cell, with a connective-tissue capsule. III, ganglionic cell, with *o*, a spiral, and *n*, straight process; *m*, sheath.

they belong to the fibre itself. These fibres also *branch* and form an anastomosing network in the course of a nerve (fig. 447). This the medullated fibres never do. These fibres, when acted on by silver nitrate, never show any crosses. The branched forms occur in the ordinary nerves of distribution, and they are numerous in the vagus, but the olfactory nerves have a distinct sheath which is nucleated.]

(2) **Medullated fibres** occur also in several forms :—

4. **Axis-cylinders**, or nerve-fibrils, **covered only by a medullary sheath**, or white substance of Schwann, are met with in the white and grey matter of the central nervous system, in the optic and auditory nerves. These *medullated nerve-fibres, without any neurilemma*, often show after death varicose swellings in their course [due to the accumulation of fluid between the medulla of myelin and the axis-cylinder]. Hence they are called **varicose fibres**. [The varicose appearance is easily produced by squeezing a small piece of the white matter of the spinal cord between a slide and a cover-glass. These fibres form the white matter of the spinal cord and brain, and it was formerly stated that nitrate of silver did not reveal any crosses, and that there are no nodes of Ranvier. Recent researches, however, have shown that these fibres of the cord are provided with Ranvier's nodes and also with incisures. When acted upon by coagulating reagents, *e.g.*, chromic acid, the medullary sheath appears laminated, so that on transverse section, when the axis-cylinder is stained, it is surrounded by concentric circles (fig. 447).

5. **Medullated Nerve-Fibres with Schwann's Sheath** (fig. 446, 5, 6). —These are the most complex nerve-fibres, and are 10 to 22·6 μ [$\frac{1}{12000}$ to $\frac{1}{3500}$ inch] broad. They are most numerous in, and in fact they make up the great mass of, the cerebro-spinal nerves, although they are also present in the sympathetic nerves.

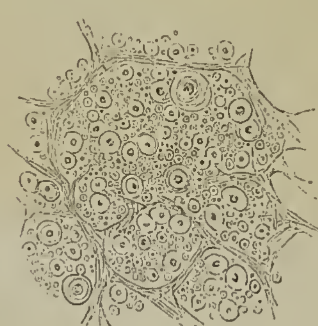


Fig. 447.

Fig. 448.

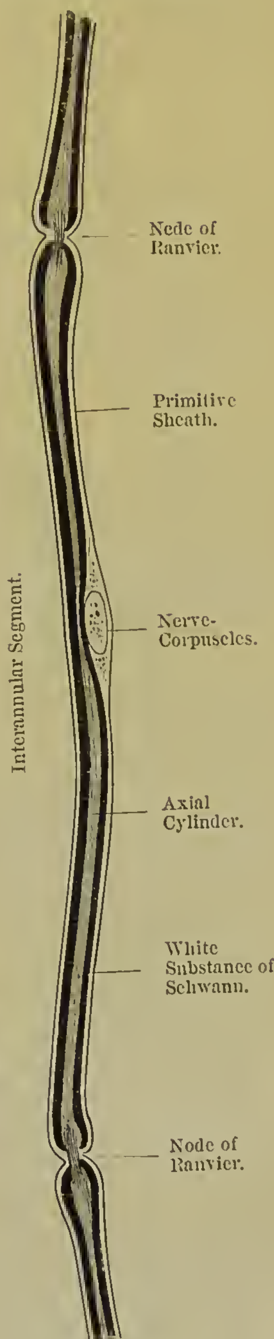


Fig. 449.

Fig. 447.—Transverse section of the nerve-fibres of the spinal cord, the axis-cylinders like dots surrounded by a clear space (myelin). Fig. 448.—Remak's fibre from vagus of dog. *b*, fibrils ; *n*, nucleus ; *p*, protoplasm surrounding it. Fig. 449.—Scheme of a medullated nerve-fibre of a rabbit acted on by osmic acid ; the incisures are omitted. × 400.

[When examined in the fresh and living condition *in situ*, they appear refractive and homogeneous (*Ranvier*, *Stirling*) ; but if acted upon by reagents, they are not

only refractive, but exhibit a **double contour**, the margins being dark and well defined.] Each fibre consists of—

[1. **Schwann's sheath**, neurilemma, or primitive sheath ;
2. **White substance of Schwann**, medullary sheath, or myelin ;
3. **Axis-cylinder** composed of fibrils and surrounded by a sheath called the **axilemma** ;
4. **Nerve-corpuscles.**]

A. The axis-cylinder, which occupies $\frac{1}{4}$ to $\frac{1}{3}$ of the breadth of the fibre, is the essential part of the nerve, and lies in the centre of the fibre like the wick in the centre of a candle (fig. 446, 6, *a*). Its usual shape is cylindrical, but sometimes it is flattened or placed eccentrically—[this is most probably due to the hardening process employed]. It is composed of **fibrils** [united by cement or stroma; they become more obvious near the terminations of the nerve, or after the action of reagents, which sometimes cause the fibrils to appear beaded. It is quite transparent, and stains deeply with carmine or logwood], while during life its *consistence* is semi-fluid. According to Kupffer, a fluid—"**neuro-plasma**"—lies between the fibrils [while, according to other observers, the whole cylinder is enclosed in an elastic sheath peculiar to itself and composed of neuro-keratin. This sheath is called by Kühne, the **axilemma.** Each axis-cylinder is an enormously long process of a ganglionic cell]. Chloroform and collodion render it visible, while it is most easily isolated as a solid rod by the action of nitric acid with excess of potassium chlorate.

Frommann's Lines.—When acted on by silver nitrate, Frommann observed transverse markings on the axis-cylinder, but their significance is unknown (fig. 446, 8). [These markings consist of alternate darker and lighter narrow transverse bars on the axis-cylinder, and are seen when a nerve is steeped for a long time in silver nitrate. They are readily made visible in this way in the nerve-fibres of the spinal cord, and, indeed, in the nerve-cells of the cord.]

B. The white substance of Schwann, medullary sheath or **myelin**, surrounds the axis-cylinder, like an insulating medium around a telegraph wire. In the perfectly fresh condition it is quite homogeneous, highly glistening, bright, and refractive ; its consistence is semi-fluid, so that it oozes out of the cut ends of the fibres in spherical drops (fig. 446, *x*), [**myelin drops**, which are always marked by concentric lines, are highly refractive, and best seen when a fresh nerve is teased in salt solution]. After death, or after the action of reagents, it shrinks slightly from the sheath, so that the fibres have a **double contour**, while the substance itself breaks up into smaller or larger droplets, due not to coagulation (*Pertik*), but, according to Toldt, to a process like emulsification, the drops pressing against each other. Thus, the fibre is broken up into masses, so that it has a characteristic appearance (fig. 446, 6). It contains a large amount of *cerebrin* and *lecithin*, which swell up to form myelin-like forms in warm water. It also contains fatty matter, so that these fibres are blackened by osmic acid, [while boiling ether extracts cholesterin from them]. Chloroform, ether, and benzin, by dissolving the fatty and some other constituents of the fibres, make them very transparent. [Some observers describe a fluid lying between the medulla and the axis-cylinder.]

C. The Sheath of Schwann, or the **neurilemma**, lies immediately outside of and invests the white sheath (fig. 446, 6, *c*), and is a delicate structureless membrane, comparable to the sarcolemma of a muscular fibre.

D. Nerve-Corpuscles.—At fairly wide intervals under the neurilemma, and lying in depressions between it and the medullary sheath, are the nucleated **nerve-corpuscles**, which are readily stained by pigments (fig. 449). [They may be compared to the muscle-corpuscles, the nuclei being surrounded by a small amount of protoplasm which sometimes contains pigment. They are not so numerous as in

muscle.] [Adamkiewicz describes nerve-corpuscles, or "**demilunes**" under the neurilemma, quite distinct from the ordinary nerve-corpuscles. They are stained yellow by saffranin, while the ordinary nerve-corpuscles are stained by methyl-anilin.]

Ranvier's Nodes or **Constrictions.**—The neurilemma forms in broad fibres at longer, and in narrower ones at shorter intervals, the **nodes** or **constrictions of Ranvier** (fig. 446, 6, *t*, *t*; fig. 449; fig. 450, *fs*). They are constrictions which occur at regular intervals along a nerve-fibre; at them the white substance of Schwann is interrupted, so that the sheath of Schwann lies upon the axis-cylinder [or its elastic sheath] at the nodes. The part of the nerve lying between any two nodes is called an **interannular** or **inter-nodal segment**, and each such segment contains one or more nuclei, so that some observers look upon the whole segment as equivalent to one cell.

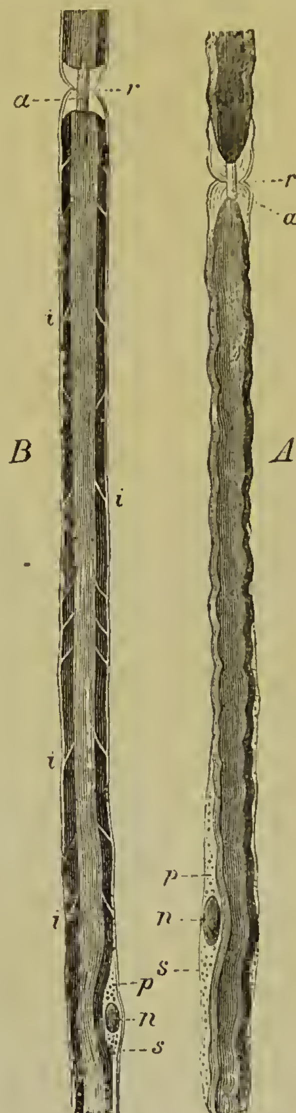


Fig. 451.

Medullated nerve-fibres (with osmic acid). *a*, axis-cylinder; *s*, sheath of Schwann; *n*, nucleus; *p*, *p*, granular substance at the poles of the nucleus; *r*, *r*, Ranvier's nodes where the medullary sheath is interrupted and the axis-cylinder appears; *i*, *i*, incisures of Schmidt.

The function of the nodes seems to be to permit the diffusion of plasma through the outer sheath into the axis-cylinder, while the decomposition-products are similarly given off. [A colouring-matter like picro-carmine diffuses into the fibre only at the nodes, and stains the axis-cylinder red, although it does not diffuse readily through the white substance of Schwann.]

Fig. 450.

Medullated nerve-fibres blackened by osmic acid. *fs*, Ranvier's node; *sch*, Schwann's sheath.

Incisures (of Schmidt and Lantermann).—Each interannular segment in a stretched nerve shows, running across the white substance, a number of oblique lines, which are called **incisures** (figs. 450, 451). They indicate that the segment is built up of a series of conical sections, each of which is bevelled at its ends, and the bevels are arranged in an imbricate manner, the one over the other, while the slight interval between them appears as an incisure. Each such section of the white matter is called a **cylinder cone** (*Kuhnt*).

Neuro-Keratin Sheath.—According to Ewald and Kühne, the axis-cylinder, as well as the white substance of Schwann, is covered with an excessively delicate sheath, consisting of *neuro-keratin*, and the two sheaths are connected by numerous transverse and oblique fibrils, which permeate the white substance. [The myelin seems to lie in the interstices of this meshwork.]

[**Rod-like Structures in Myelin.**—If a nerve be hardened in *ammonium chromate* (or *picric acid*), M'Carthy has shown that the myelin exhibits rod-like structures radiating from the axis-cylinder outwards, which are stained with logwood and carmine. The rods are probably not distinct from each other, but are perhaps part of the neuro-keratin network already described.]

Action of Nitrate of Silver.—When a small nerve, *e.g.*, the intercostal nerve of a mouse, is acted on by silver nitrate, it is seen to be covered by an endothelial sheath composed of flattened endothelial cells (fig. 452), while the nerve-fibres themselves exhibit **crosses** along their course. These crosses are due to the penetration of the silver solution at the nodes, where it stains the cement-substance and also part of the axis-cylinder, so that the latter sometimes exhibits transverse markings called **Frommann's lines** (fig. 446, 8).]

Fig. 452.

Intercostal nerve of a mouse (single fasciculus of nerve-fibres) stained with silver nitrate. Endothelial sheath stained, and some nodes of Ranvier indicated by crosses.

[**New Methods.**—Much progress has recently been made in tracing the course of medullated nerve-fibres by the action of new staining reagents; thus acid fuchsin stains the myelin deeply, leaving the other parts unstained; at least, it can be so manipulated as to yield this result. **Weigert's Method** and its modifications have yielded most important results, and proved that medullated nerve-fibres exist in many parts of the central nervous system where they cannot be seen in the ordinary way. The nerve-tissue is hardened in a solution of a chromium salt, and placed in a half-saturated solution of cupric acetate; it is then stained with logwood, and afterwards the elements are differentiated by steeping the sections in a solution of ferricyanide of potash and borax. The myelin is coloured a logwood tint.]

In the spinal nerves, those fibres are thickest which have the longest course before they reach their end-organ (*Schwalbe*), while those ganglion-cells are largest which send out the longest nerve-fibres (*Pierret*). [Gaskell finds that the longest nerves are not necessarily the thickest, for the visceral nerves in the vagus are small nerves, and yet run a very long course.]

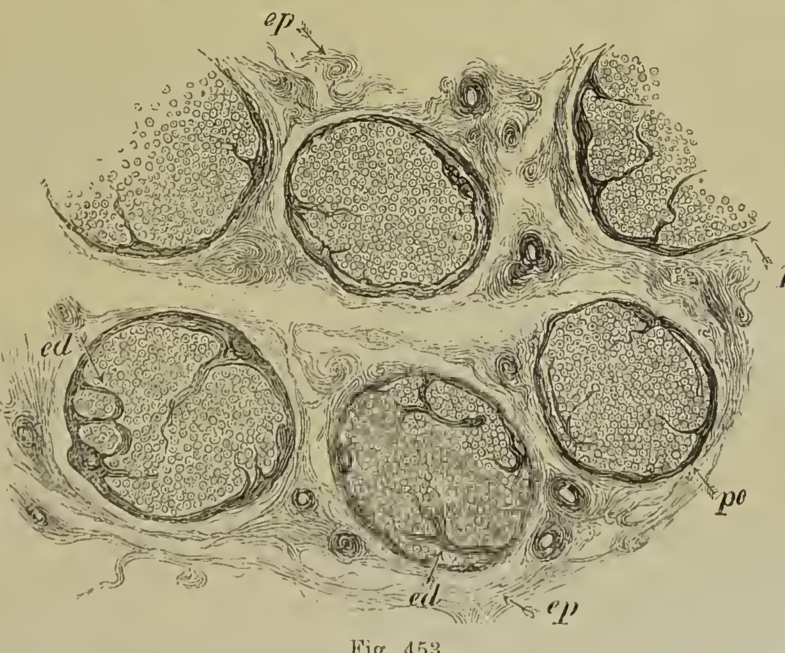


Fig. 453.

Trans. section of a nerve (median). *ep*, epineurium; *pe*, perineurium; *ed*, endoneurium.

Division of Nerves.—Medullated nerve-fibres run in the nerve-trunks without dividing; but when they approach their termination they often divide dichotomously [at a node], giving rise to two similar fibres, but there may be several branches at a node (fig. 454, *t*). [The divisions are numerous in motor nerves to striped muscles.] In the **electrical nerves** of the malapterurus and gymnotus, there is a great accumulation of Schwann's sheaths round a nerve, so that a nerve-fibre is as thick as a sewing-needle. Such a fibre, when it divides, breaks up into a bundle of smaller fibres.

[**Nerve-Sheaths.**—A nerve-trunk consists of **bundles**, or **fasciculi**, of nerve-fibres. The bundles are held together by a common connective-tissue sheath (fig. 453, *ep*), the **epineurium** [sometimes called the perineurium externum, general perineurium, or in the older writers neurilemma], which contains the larger blood-vessels, lymphatics, and sometimes fat and plasma cells. Each bundle is surrounded with its own sheath or **perineurium** (*pe*), which consists of lamellated connective-tissue disposed circularly, and between the lamellæ are lymph-spaces lined by flattened endothelial plates. These lymph-spaces may be injected from and communicate with the lymphatics (*Key and Retzius*).] The nerve-fibres within any bundle are held together by delicate connective-tissue, which penetrates between the adjoining fibres, constituting the **endoneurium** (*ed*). It consists of delicate fibres with branched connective-tissue corpuscles (fig. 446, 6, *d*), and in it lie the capillaries, which are not very numerous, and are arranged to form elongated open meshes.

[**Henle's Sheath.**—When a nerve is traced to its distribution, it branches and becomes smaller, until it may consist only of a few bundles or even a single bundle of nerve-fibres. As the bundle branches, it has to give off part of its lamellated sheath or perineurium to each branch, so that, as we pass to the periphery, the smaller bundles are surrounded by few lamellæ. In a bundle containing only a few fibres, this sheath may be much reduced, or may consist only of thin, flattened, connective-tissue corpuscles with a few fibres. A sheath surrounding a few nerve-fibres is called *Henle's Sheath* by Ranvier.]

[**Nervi Nervorum.**—Marshall and V. Horsley have shown that the nerve-sheaths are provided with special nerve-fibres, in virtue of which they are endowed with sensibility.]

Development of Nerve-Fibres.—At first nerve-fibres consist only of fibrils, *i.e.*, of axis-cylinders, which become covered with connective substance, and ultimately the white substance of Schwann is developed in some of them. The growth in length of the fibres takes place by elongation of the individual "interannular" segments, and also by the new formation of these (*Vignal*). [Medullated nerve-fibres are derived from the **epiblast**. The axis-cylinders of those of the anterior root grow from, and are in reality, the axis-cylinders of nerve-cells—called **neuroblasts** in their early stage. The fibres of the posterior root of a spinal nerve grow from the nerve-cells or neuroblasts of the rudiment of the spinal ganglion. The axis-cylinder processes, which ultimately form the fibres of the anterior roots, appear about the fourth week of the human fœtus. They grow slowly and do not reach the tips of the toes or fingers until after the second month (*His*).]

II. Ganglionic or **Nerve-Cells** [vary much in size and general characters. They may have one pole, when they are **unipolar** (spinal ganglion cells); or two poles—**bipolar** (spinal ganglion cells of fishes); or many poles, when they are **multipolar** (cells of the spinal cord).]—1. **Multipolar nerve-cells** (fig. 446, I) occur partly as *large* cells (100 μ), and are visible to the unaided eye, as in the anterior horn of the spinal cord, and in a different form in the cerebellum, and partly in a *smaller* form (20 to 10 μ) in the posterior horns of the spinal cord, many parts of the cerebrum and cerebellum, and in the retina. They may be spherical, ovoid, pyramidal [cerebrum], pear- or flask-shaped [cerebellum]. (1) Each cell is provided with **numerous branched processes**, which gives the cells a characteristic appearance. [Deiters isolated such cells from the anterior horn of the grey matter of the spinal cord, so that this special form of cell is sometimes called "Deiters' cell" (fig. 446, I).] Those of the spinal cord are devoid of a cell envelope, are of soft consistence, and exhibit a fibrillated structure, which may extend even into the processes. Fine granules lie scattered throughout the cell-substance between the fibrils. Not

unfrequently yellow or brown granules of pigment are also found, either collected at certain parts in the cell or scattered throughout it. The relatively large **nucleus** consists of a clear envelope enclosing a resistant substance. It does not appear to have a membrane in youth (*Schwalbe*). Within the nucleus lies the **nucleolus**, which in the recent condition is angular, provided with processes and capable of motion, but after death is highly refractive and spherical. (2) Each cell is provided with **one unbranched process**, constituting the **axial-cylinder process** (I, *z*) which remains unbranched, but it soons becomes covered with the white substance of Schwann, and the other sheaths of a medullated nerve, so that it becomes the axial cylinder of a nerve-fibre. Thus a nerve-fibre is merely an excessively long, unbranched process of a nerve-cell pushed outwards towards the periphery.] It is now definitely ascertained that the cerebral cells have such processes. All the other processes divide very frequently until they form a branched, root-like, complex arrangement of the finest primitive fibrils. These are called **protoplasmic processes** (I, *y*). By means of these processes it is supposed adjoining cells are brought into communication with each other, so that impulses can be conducted from one cell to another. Further, many of these fibrils approximate to each other, and join together to form axis-cylinders of other nerve-fibres. The most recent observers, however, state that the processes of neighbouring cells do not anastomose, they merely come into relation with each other. [V. Thanhoffer states that he has traced the axis-cylinder process to the nucleus and nucleolus.]

[His, Forel, and other observers deny the existence of these anastomoses. The processes of adjoining nerve-cells merely approach each other, but do not actually unite with each other, there being always an intermediate substance between them.]

2. **Bipolar cells** are best developed in **fishes**, *e.g.*, in the spinal ganglia of the skate, and in the Gasserian ganglion of the pike. They appear to be nucleated, fusiform enlargements of the axis-cylinder (fig. 446, on the right of I). The white substance often stops short on each side of the enlargement, but sometimes the white substance and the sheath of Schwann pass over the enlargement.

Fig. 454.

Cell from the Gasserian ganglion. *n*, nuclei of the sheath; *t*, fibre dividing at a node of Ranvier.

3. **Nerve-cells with connective-tissue capsules** occur in the peripheral ganglia of man (fig. 446, II). The soft body of the cell, which is provided with several processes, is covered by a thick, tough capsule composed of several layers of connective-tissue corpuscles; while the inner surface of the composite capsule is lined by a layer of delicate endothelial cells (fig. 454). The body of the cells in the spinal ganglia is traversed by a network of fine fibrils (*Flemming*). The capsule is continuous with the sheath of the nerve-fibre.

Rawitz and G. Retzius find that the cells of the spinal ganglia are **unipolar**, the outgoing fibre taking a half-turn within the capsule before it leaves the cell (fig. 454). Retzius [and Ranvier] observed the process to divide like a T. Perhaps this division corresponds to the two processes of a bipolar cell. The jugular ganglion and plexus gangliiformis vagi in man contain only unipolar cells, so that,

in this respect, they may be compared to spinal ganglia. The same is the case in the Gasserian ganglion; while the ciliary, spheno-palatine, otic, and submaxillary ganglia structurally resemble the ganglia of the sympathetic.

4. **Ganglionic cells with spiral fibres** occur chiefly in the abdominal sympathetic of the frog (*Beale*, *J. Arnold*). The body of the cell is usually pyriform in shape, and from it proceeds an unbranched **straight process** (fig. 446, III, *n*), which ultimately becomes the axis-cylinder of a nerve. A **spiral fibre** springs from the cell (? a network), emerges from it, and curves in a spiral direction round the former (*o*). The whole cell is surrounded by a nucleated capsule (*m*). We know nothing of the significance of the different fibres. According to Ehrlich, the straight fibres conduct in a centrifugal and the spinal process in a centripetal direction.

[Some light has recently been thrown upon the structure of the pyriform cells of the frog, by the use of **methylene-blue** (*Ehrlich*, *Feist*, *Smirnow*). This substance stains certain parts of the cell when it is injected into the blood, and the stain can afterwards be fixed. The capsule remains colourless, and from the body of the cell there arises a **straight fibrillated process.** Round the cell are a number of fine fibrils, **pericellular fibrils**, which unite to form the **spiral fibre**, which is much finer than the former, and stains blue with methylene blue when exposed to the air. Usually all the straight fibres from adjoining cells run in one direction, and all straight fibres in the opposite direction.]

322. CHEMICAL AND MECHANICAL PROPERTIES OF NERVOUS SUBSTANCE.—1. **Proteids.**—Albumin occurs chiefly in the axis-cylinder and in the substance of the ganglionic cells. Some of this proteid substance presents characters not unlike those of myosin (§ 293). Dilute solution of common salt extracts a proteid from nervous matter, which is precipitated by the addition of much water and also by a concentrated solution of common salt (*Petrowsky*). *Potash-albumin* and a *globulin-like substance* are also present. [Halliburton finds that the proteids of nervous matter are all globulins; albumins, albumoses, and peptones being absent.] **Nuclein** occurs especially in the grey matter (§ 250, 2), while **neuro-keratin**, a body containing much sulphur and closely related to keratin, occurs in the corneous sheath of nerve-fibres (p. 652). If grey nervous matter be subjected to artificial digestion with trypsin, both of these substances remain undigested (*Kühne and Ewald*). Pure neuro-keratin is obtained by treating the residue with caustic potash. The **sheath of Schwann** does not yield gelatin, but a substance closely related to *elastin* (§ 250, 6), from which it differs, however, in being more soluble in alkalies. The connective-tissue of nerves yields gelatin.

2. **Fats** *and other allied substances soluble in ether*, more especially in the white matter:—

(*a*) **Protagon**, which contains N and P, is similar to cerebrin, and is, according to its discoverer, the chief constituent of the brain (*Liebreich*).

According to Hoppe-Seyler and Diaconow, it is a mixture of lecithin and cerebrin. [The investigations of Gamgee and Blankenhorn have shown, however, that protagon is a definite chemical body. They find that, instead of being unstable, it is a very stable body.] It is a glucoside, and crystalline, and can be extracted from the brain by warm alcohol, and when boiled with baryta yields the decomposition-products of lecithin.

(*b*) **Cerebrin**, free from phosphorus (§ 250, 3).

Cerebrin is a white powder composed of spherical granules soluble in hot alcohol and ether, but insoluble in cold water. It is decomposed at 80° C., and its solutions are neutral. When boiled for a long time with acids, it splits up into a left-rotatory body like sugar, and another unknown product. **Preparation.**—Rub up the brain into a thin fluid with baryta water. Extract the separated coagulum with boiling alcohol. The extract is frequently treated with cold ether to remove the cholesterin (*W. Müller*). Parkus separated from cerebrin its homologue, **homocerebrin**, which is slightly more soluble in alcohol, and the clyster-like body, **encephalin**, which is soluble in hot water.

(*c*) **Lecithin** and its decomposition-products—glycero-phosphoric acid and oleo-phosphoric acid (§ 251).

Lecithin is an ethereal compound of neurin, in which the latter takes the place of the alcohol. Neurin (or Cholin = $C_5H_{15}NO_2$) is a strongly alkaline, colourless fluid, forming crystalline salts with acids. It is soluble in water and alcohol, and has been formed synthetically from glycol and trimethylamin. Lecithin is a salt of the base neurin.

3. The following substances are **extracted by water**:—Xanthin and hypoxanthin (*Scherer*), kreatin (*Lerch*), inosit (*W. Müller*), ordinary lactic acid (*Gscheidlen*), acetic and formic acids, uric acid (?), and volatile fatty acids; leucin (in disease), urea (in uræmia), and a substance like starch in the human brain (*Jaffé*). All these substances are for the most part products of the regressive metabolism of the tissues.

Reaction.—Nervous substance, when passive, is neutral or feebly alkaline in reaction, while active (? and dead) it is acid (*Funke*). The grey matter of the brain, when quite fresh, is alkaline (*Liebreich*), but death rapidly causes it to become acid (*Gscheidlen*).

The reaction of nerve-fibres varies during life. After introducing **methylene-blue** into the body of a living animal, Ehrlich found that the axis-cylinder became blue, *i.e.*, in those nerves which have an alkaline reaction.

The nerves after death have a more solid consistence, so that in all probability some coagulation or change, "**nerve rigor**," comparable to the stiffening of muscle, occurs in them after death, while at the same time a free acid is liberated (§ 295). If a fresh brain be rapidly "broiled" at 100° C., it, like a muscle similarly treated, remains alkaline (§ 295).

Chemical Composition of	Grey Matter.	White Matter.
Water,	81·6 per cent.	68·4 per cent.
Solids,	18·4 ,,	31·6 ,,
The solids consist of—		
Proteids (Globulins),	55·4 ,,	24·7 ,,
Lecithin,	17·2 ,,	9·9 ,,
Cholesterin and fats,	18·7 ,,	52·1 ,,
Cerebrin,	0·5 ,,	9·5 ,,
Substances insoluble in ether,	6·7 ,,	3·3 ,,
Salts,	1·5 ,,	0·5 ,,
	100·0	100·0

In 100 parts of **ash**, Breed found **potash** 32, soda 11, magnesia 2, lime 0·7, NaCl 5, iron phosphate 1·2, fixed **phosphoric acid** 39, sulphuric acid 0·1, silicic acid 0·4.

[Ptomaines (§ 166) are obtained from putrefying brain. They have an effect on the motor nerves like curare, but in much less degree, while the phenomena last for a much shorter time (*Guareschi and Mosso*).]

Mechanical Properties.—One of the most remarkable mechanical properties of nerve-fibres is the absence of elastic tension according to the varying positions of the body. Divided nerves do not retract; such nerves exhibit delicate, microscopic, transverse folds [like watered silk], or Fontana's transverse markings.

The **cohesion** of a nerve is very considerable. When a limb is forcibly torn from the body, as sometimes happens from its becoming entangled in machinery, the nerve not unfrequently remains unsevered, while the other soft parts are ruptured. [Tillaux found that a weight of 110 to 120 lbs. was required to rupture the sciatic nerve at the popliteal space, while to break the median or ulnar nerve of a fresh body, a force equal to 40 to 50 lbs. was required. The toughness and elasticity of nerves are often well shown in cases of injury or gun-shot wounds. The median or ulnar nerve will gain 15 to 20 centimetres (6 to 8 inches) before breaking. Weir Mitchell has shown that a healthy nerve will bear a very considerable amount of pressure and handling, and, in fact, the method of nerve-stretching depends upon this property of a nerve-trunk.]

323. METABOLISM OF NERVES.—**Influence of Blood-Supply.**—We know very little regarding the metabolic processes which take place in nerve-tissue. Some **extractives** are obtained from nerve-tissue, and they may, perhaps, be regarded as decomposition-products (p. 657). It has not been proved satisfactorily that during the activity of nerves there is an exchange of O and CO_2. That there is an exchange of materials within the nerves is proved by the fact that, after **compression of the blood-vessels** of the nerves, the excitability of the nerves falls, and is restored again when the circulation is re-established. Compression of the abdominal aorta causes paralysis and numbness of the lower half of the body while occlusion of the cerebral vessels causes almost instantaneously cessation of the cerebral functions. The metabolism of the central nervous organs is much more active than that of the nerves themselves. [If the abdominal aorta of a rabbit be compressed for a few minutes, the hind limbs are quickly paralysed, the animal crawls forward on its fore-legs, drawing the hind limbs in an extended position after it.] The ganglia form much lymph. According to Hodge, the cells of the spinal ganglia when they are stimulated, [*i.e.*, by stimulating the central end of a divided spinal nerve with an electrical current] can be distinguished from resting ganglionic cells, by their smaller size, the presence of vacuoles in their protoplasm as well as by their smaller nuclei.

324. EXCITABILITY OF THE NERVES—STIMULI.—Nerves possess the property of being thrown into a state of excitement by **stimuli**, and are, therefore, said to be **excitable** or irritable. The stimuli may be applied to, and may act upon, any part of the nerve. [Such stimuli as act on a nerve in any part of its course are called **general stimuli**. The following are the various kinds of **general stimuli**, *i.e.*, modes of motion, which act upon nerves:—

1. Mechanical, *e.g.*, pinching.
2. Thermal, *e.g.*, suddenly raising its temperature.
3. Chemical, *e.g.*, dilute acids and alkalies.
4. Physiological.
5. Electrical, *e.g.*, an induction shock.

1. **Mechanical stimuli** act upon nerves when they are applied with sufficient rapidity to produce a change in the form of the nerve-particles, *e.g.*, a blow, pressure, pinching, tension, puncture, and section. In the case of **sensory** nerves, when they are stimulated, **pain** is produced, as is felt when a limb "sleeps," or when pressure is exerted upon the ulnar nerve at the bend of the elbow. When a **motor** nerve is stimulated, **motion** results in the muscle attached to the nerve. If the continuity of the nerve-fibres be destroyed, or, what is the same thing, if the continuity of the axial cylinder be interrupted by the mechanical stimulus, the *conduction* of the impulse across the injured part is interrupted. If the molecular arrangements of the nerves be permanently deranged, *e.g.*, by a violent shock, the excitability of the nerves may be thereby extinguished.

A slight blow applied to the radial nerve in the fore-arm, or to the axillary nerves in the supraclavicular groove, is followed by a contraction of the muscles supplied by these nerves. Under pathological conditions, the excitability of a nerve for mechanical stimuli may be increased enormously.

Tigerstedt ascertained that the **minimal mechanical stimulus** is represented by 900 milligram-millimetres, and the **maximum** by 7000 to 8000. Strong stimuli cause fatigue, but the fatigue does not extend beyond the part stimulated. A nerve when stimulated mechanically does not become acid. Slight pressure without tension increases the excitability, which diminishes after a short time. The mechanical work produced by an excited muscle in consequence of a stimulus was 100 times greater than the mechanical energy of the mechanical nerve-stimulus.

Continued pressure upon a **mixed nerve** paralyses the motor sooner than the sensory fibres. If the stimulus be applied *very gradually*, the nerve may be rendered inexcitable without manifesting any signs of its being stimulated (*Fontana*, 1758). Paralysis, due to continuous pressure gradually applied, may

occur in the region supplied by the branchial nerves; the left recurrent laryngeal nerve also may be similarly paralysed from the pressure of an aneurism of the arch of the aorta.

By increasing the pressure on a nerve by using a gradually increasing weight, there is at first an increase and then a decrease of the excitability. Pressure on a mixed nerve abolishes reflex conduction sooner than motor conduction (*Kronecker and Zederbaum*).

Nerve-stretching is employed for therapeutical purposes. If a nerve be exposed and stretched, or if it be made sufficiently tense, the nerve is stimulated. Slight tension increases the reflex excitability (*Schleich*), while violent extension produces a temporary diminution or abolition of the excitability (*Valentin*). The centripetal or sensory fibres of the sciatic nerve are sooner paralysed thereby than the centrifugal or motor (*Conrad*). During the process of extension, mechanical changes are produced, either in the nerve itself or in its end-organs, causing an alteration of the excitability, but it may also affect the central organs. The paralysis, which sometimes occurs after forcible stretching, usually rapidly disappears. Therefore, when a nerve is in an excessively excitable condition, or when this is due to an inflammatory fixation or constriction of the nerve at some part of its course, nerve-stretching may be useful, partly by diminishing the excitability, partly by breaking up the inflammatory adhesions. In cases where stimulation of an afferent nerve gives rise to *epileptic* or *tetanic spasms*, nerve-stretching may be useful by diminishing the excitability at the periphery, in addition to the other effects already described. It has also been employed in some spinal affections, which may not as yet have resulted in marked degenerative changes.

Tetanomotor.—For physiological purposes, a nerve may be stimulated mechanically by means of Heidenhain's **tetanomotor**, which is simply an ivory hammer attached to the prolonged spring of a Neef's hammer of an induction machine. [A more delicate form of this instrument was used by Tigerstedt (§ 335).] The rapid vibration of the hammer communicates a series of mechanical shocks to the nerve upon which it is caused to beat. Rhythmic extension of a nerve causes contractions and even tetanus.

2. **Thermal Stimuli.**—If a frog's nerve be **heated** to 45° C., its *excitability* is first increased and then diminished. The higher the temperature, the greater is the excitability, and the shorter its duration (*Afanasieff*). If a nerve be heated to 50° C. for a short time, its excitability and conductivity are abolished. The frog's nerve alone regains its excitability on being cooled (*Pickford*). If the temperature be raised to 65° C., the excitability is abolished without the occurrence of a contraction, while its medulla is broken up (*Eckhard*). Sudden cooling of a nerve to 5° C. acts as a stimulus, causing contraction, in a muscle, while sudden heating to 40° or 45° C. produces the same result. If the temperature be increased still more, instead of a single contraction a tetanic condition is produced. All such rapid variations of temperature quickly exhaust the nerve and kill it. If a nerve be frozen gradually, it retains its excitability on being thawed. The excitability lasts long in a **cooled nerve**; in fact, it is increased in a motor nerve, but the contractions are not so high and more prolonged, while the conduction in the nerve takes place more slowly. Amongst *mammalian* nerves, the afferent and vaso-dilator nerves at 45° to 50° C. exhibit the results of stimulation, while the others only show a change in their excitability. When cooled to + 5° C., the excitability of all the fibres is diminished (*Grützner*).

3. **Chemical Stimuli** excite nerves when they act with a certain rapidity, and thereby alter the condition of the nerve (p. 588). Most chemical stimuli act by first increasing the nervous excitability, and then diminishing or paralysing it. Chemical stimuli, as a rule, have less effect upon *sensory* than upon motor fibres (*Eckhard*). According to Grützner, the inactivity of chemical stimuli, so often observed when they are applied to sensory nerves, depends in great part upon the non-simultaneous stimulation of all the nerve-fibres. Amongst chemical stimuli are—(*a*) **rapid abstraction of water** by dry air, blotting-paper, exposure in a chamber containing sulphuric acid, or by the action of solutions which absorb fluids, *e.g.*, concentrated solutions of neutral alkaline salts (NaCl excites only motor fibres in mammals—*Grützner*), sugar, urea, concentrated glycerin (and ? some metallic salts). The subsequent addition of water may abolish the contractions, while the nerve may still remain excitable. The abstraction of water first increases

and afterwards diminishes the excitability. The *imbibition of water* diminishes the excitability. (*b*) Free **alkalies**, mineral **acids** (not phosphoric), many organic acids (acetic, oxalic, tartaric, lactic), and most salts of the heavy metals. While the acids act as stimuli, only when they are somewhat concentrated, the caustic alkalies act in solutions of 0·8 to 0·1 per cent. (*Kühne*). Neutral potash salts, in a concentrated form, rapidly kill a nerve, but they do not excite it nearly so strongly as the soda compounds. Dilute solutions of the neutral potash salts first increase and afterwards diminish it (*Ranke*), as can be shown by stimulation with an induction shock (*Biedermann*). (*c*) **Various chemical substances,** *e.g.*, dilute alcohol, ether, chloroform, bile, bile-salts, and sugar. These substances usually excite contractions, and afterwards rapidly kill the nerve. Ammonia, lime-water, some metallic salts, carbon bisulphide, and ethereal oils kill the nerve without exciting it—at least without producing any contraction in a frog's nerve-muscle preparation. [The nerve of a nerve-muscle preparation may be dipped into ammonia, but no contraction results, while the slightest traces of ammonia applied to a muscle cause contraction.] Carbolic acid does the same, although when applied directly to the spinal cord it produces spasms. These substances excite the muscles when they are directly applied to them. Tannic acid does not act as a stimulus either to nerve or muscle. As a general rule, the stimulating solution must be more *concentrated* when applied to a nerve than to muscle, in order that a contraction may be produced.

[**Methods.**—If a nerve-muscle preparation of a frog's limb be made, and a straw flag (p. 587) attached to the toes while the femur is fixed in a clamp, and its nerve be then dipped in a saturated solution of common salt, the toes soon begin to twitch, and by and by the whole limb becomes tetanic, and thus keeps the straw flag extended. The effect of fluid on a muscle or nerve is easily tested by fixing the muscle in a clamp, while a drop of the fluid is placed on a greased surface, which gives it a convex form. The end of the muscle or nerve is then brought into contact with the cupola of the drop (*Kühne*).]

4. **The Physiological** or **normal stimulus** excites the nerves in the normal intact body. Its nature is entirely unknown. The "**nerve-motion**" thereby set up travels either in a "**centrifugal**" or **efferent** or outgoing direction from the central nervous system, giving rise to motion, inhibition of motion, or secretion; or in a "**centripetal**" or **afferent** or ingoing direction from the specific *end-organs* of the nerves of the special senses or the sensory nerves. In the latter case, the impulse reaches the central organs, where it may excite sensation or perception, or it may be transferred to the motor areas, and be conducted in a centrifugal direction, constituting a "**reflex stimulation**" (§ 360). A single physiological nerve-impulse travels more slowly than that excited by the momentary application of an induction shock (*Lovèn, v. Kries*). It is not a uniform process excited by varying intensity and greater or less frequency of stimulation, but it is essentially a process varying considerably in duration, and it may even last as long as $\frac{1}{8}$ second (*v. Kries*).

5. **Electrical Stimuli.**—[The following forms of electrical stimuli may be used:—

(1) **Constant current,** which may be made or broken (§ 328).
(2) **Induction shocks,** either make or break shocks (§ 329).
(3) **Interrupted current** (§ 329).]

The electrical current acts most powerfully upon the nerves at the moment when it is *applied*, and at the moment when it *ceases* (§ 336); in a similar way, any increase or decrease in the strength of a constant current acts as a stimulus. If an electrical current be applied to a nerve, and its strength be very gradually increased or diminished, then the visible signs of stimulation of the nerve are very slight. As a general rule, the stimulation is more energetic the more rapid the variations of the strength of the current applied to the nerve, *i.e.*, the more suddenly the **intensity** of the stimulating current is increased or diminished (*du Bois-Reymond*).

An electrical current must have a certain **strength** or **liminal intensity** before it is effective. By uniformly increasing the strength of the current, the size of the contraction increases rapidly at first, then more slowly (*Tigerstedt and Willhard*).

An electrical current, in order to stimulate a nerve, must have a certain **duration**, it must act at least during 0·0015 second (*Fick*, 1863); even with currents of slightly longer duration, the opening shock may have no effect. If the duration of the closing shock of a constant current be so arranged that it is just too short to be active, then it merely requires to last 1·3 to 2 times longer to produce the most complete effect (*Grünhagen*).

The electrical current is most active when it flows in the **long axis** of the nerve; it is inactive when applied vertically to the axis of the nerve (*Galvani*). Similarly, muscles are incomparably less excited by transverse than by longitudinal currents (*Giuffrè*).

The *greater* the **length of nerve** traversed by the current, the *less* the stimulus that is required (*Pfaff*).

Constant Current on a Nerve.—If the constant current be used as a nervous stimulus, the stimulating effect on the **peripheral terminations of sensory nerves**, *e.g.*, tongue or skin, is most marked at the moment of making and breaking the current; during the time the current passes only slight excitement is perceived, but, even under these circumstances, very strong currents may cause very considerable, and even unbearable, sensations [*i.e.*, conformable to the rule that sudden variations in the intensity of a current act as a stimulus, there is, if the current be strong enough, a sensation on **making** (closing) or **breaking** (opening) the constant current or on both events. If, however, the current be strong, then sensations are experienced whilst the current is flowing. This is different from what obtains in motor nerves.] If a constant current be applied to a **motor nerve**, the greatest effect is produced when the current is made or closed [**closing** or **make contraction**], and when it is broken or opened [**opening** or **break contraction**]. [No contraction takes place while the current is passing. An important change takes place in the nerve all the time the constant current is flowing, viz., the condition of **electrotonus** is set up, whereby the physiological properties of the nerve are greatly modified (§ 333), but these do not concern us at present.] Under certain circumstances, however, while the current is passing, the stimulation does not cease completely, for, with a certain strength of stimulus, the muscle remains in a state of tetanus (**galvanotonus** or "**closing tetanus**") (*Pflüger*). For the effect of a constant current on **muscles**, see p. 598. With strong currents this tetanus does not appear, chiefly because the current diminishes the excitability of the nerves, and thus develops resistance, which prevents the stimulus from reaching the muscle. According to Hermann, a descending current applied to the nerve, at a distance from the muscles, causes this tetanus more readily, while an ascending current causes it more readily when the current is closed near the muscle. The constant current is said by Grützner to have no effect on **vaso-motor** and **secretory** fibres.

Over-maximal Contraction.—By gradually increasing the strength of the electrical stimulus applied to a motor nerve, Fick observed that the muscular contractions (height of the lift) at first increased proportionally to the increase of the stimulus, until a maximal contraction was obtained. If the strength of the stimulus be increased still further, another increase of the contraction above the first-reached maximum is obtained. This is called an "**over-maximal contraction.**" Occasionally between the first maximum and the second there is a diminution, or indeed absence of, or **gap** or **hiatus**, in the contractions. The cause of this lies in the positive pole, which with a certain strength of current is sufficient to prevent the further transmission of the excitement (§ 335). On continuing to increase the induction current, ultimately a stage is reached where the stimulation at the negative pole again becomes stronger than the block caused at the positive pole, and this overcomes the latter. The contractions before the gap are caused by the occurrence of the induction current (their latent period is short); the contractions (long latent period, like that after all opening shocks—*Waller*), after the gap, are

caused by the disappearance of the induction current, *i.e.*, by polarisation; this is added to the stimulation proceeding from the negative pole, which after the gap overcomes the inhibition at the positive pole, and excites the over-maximal contractions (*Tigerstedt and Willhard*).

Tetanus.—If single electrical shocks either from a constant current or induced shocks of short duration be rapidly applied after each other to a nerve, tetanus in the corresponding muscle is produced (§ 298, III.).

A motor nerve has a greater *specific* excitability for electrical stimuli than the muscle-substance. This is proved by the fact that a feebler stimulus suffices to excite a muscle when applied to the nerve than when it is applied to the muscle directly, as occurs when the terminations of the motor nerves are paralysed by curare (§ 296, 2, *Rosenthal*).

Soltmann found that the excitability of the motor nerves of **new-born** animals for electrical stimuli is less than in adults. The excitability increases until the 5th to 10th month.

Unequal Excitability of a Nerve.—Under certain circumstances, the nearer the part of the motor nerve stimulated lies to the central nervous system, the greater is the effect produced (contraction); [or what is the same thing, the further the point of a nerve which is stimulated is from the muscle, the stimulus being the same, the greater is the contraction. This led Pflüger to his "**avalanche-theory,**" *i.e.*, that the "nerve-motion" increases in the nerve as it passes towards the muscles. This effect is explained, however, by the unequal excitability of different parts of the same nerve. Suppose a motor nerve in a nerve-muscle preparation of a frog be excited with the same strength of stimulus, *e.g.*, by very weak induction shocks, at a point near the muscle, so as to obtain just a feeble contraction of the muscle, the same strength of stimulus applied at a point further away from the muscle will cause a much greater contraction in the muscle. This is not due to the nerve-impulse gaining strength as it traverses a long stretch of nerve, but is due to the fact that the excitability is greater at parts of the nerve away from the muscle than at parts nearer the muscle, *i.e.*, the **excitability is greatest** near the **nerve-centre,** probably because of the trophic influence of the nerve-cells of the spinal cord on the nerve-fibres.]

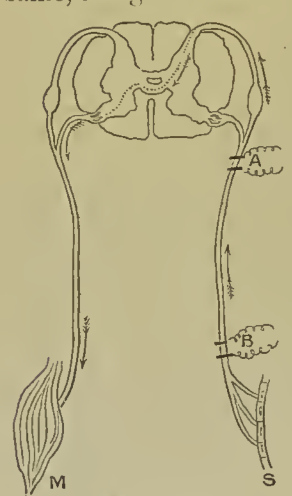


Fig. 455.

Scheme of Rutherford's experiment. *Sp. Cd*, spinal cord; *S*, afferent nerve-fibre; *M*, muscles; *El.*, electrodes at *A*, near cord, and at *B* near muscle.

[That the length of nerve is not the cause is shown by the following experiment of Rutherford on the **reflex movements** of a frog.]

[Expose the whole length of, but do not divide, one sciatic nerve of a frog in which the brain is destroyed. The sciatic nerve contains both motor and sensory fibres. On stimulating the nerve at any part of its course the limb of the opposite side contracts **reflexly.** The reflex contraction, caused on stimulating the afferent or sensory nerve-fibres at *A*, is greater than that caused by the stimulation of the nerve at *B*. In the latter case a much longer stretch of nerve is traversed by the impulse than in the former, yet the reflex contraction is greater in the former].

According to Fleischl, all parts of the nerve are equally excitable for *chemical* stimuli. Further, it is said that the higher placed parts of a nerve are more excitable only when the stimulating current passes in a descending direction; the reverse is the case when the current ascends (*Hermann*). On stimulating a *sensory* nerve, Rutherford and Hällsten found that the reflex contraction was greater the nearer the stimulated point was to the central nervous system.

Unequal Excitability in the same Nerve.—Nerve-fibres, even when functionally the same and included in the same nerve-trunk, are not all equally excitable. Thus, feeble stimulation of the sciatic nerve of a frog causes contraction of the flexor muscles, while it requires a stronger stimulus to produce contraction of the extensors (*Ritter*, 1805, *Rollett*). According to Ritter, the nerves for the flexors die first.

Direct stimulation of the muscles in curarised animals shows that the flexors contract with a feebler stimulus (but also fatigue sooner) than the extensors; the pale muscles of the rabbit are also more excitable than the red. As a rule, **poisons** affect the flexors sooner than the extensors. In some muscles some pale fibres are present, and they are more excitable than the red (*Grützner*) (§ 298). If a frog's nerve-muscle preparation be exposed to the action of ether, on strong stimulation of the sciatic nerve, flexion occurs (*Grützner*, *Bowditch*), but, if the current be made stronger, extension takes place. During deep ether-narcosis strong stimulation of the recurrent nerve causes dilatation, and with slight narcosis, narrowing of the glottis takes place; dilatation occurs on slight stimulation (*Bowditch*). The **adductor muscle** of the claw of a **crayfish** is relaxed under a weak stimulus, but it contracts when a strong stimulus is applied to it. The reverse is the case with the muscle which opens the claw (*Biedermann*).

Unipolar Stimulation.—If **one electrode** of an induction apparatus be applied to a nerve, it may act as a stimulus. Du Bois-Reymond has called this "unipolar induction action." It is due to the movement of the electrical current to and from the free ends of the open induction current at the moment of induction. [Unipolar induction is more apt to occur with the opening than the closing shock, because the former is more intense.]

Electrical Stimuli on Muscle.—Upon **muscle**, electrical stimuli act quite as they do upon nerves. Electrical currents of *very short* duration have no effect upon muscles whose nerves are paralysed by curare (*Brücke*), and the same is true of greatly fatigued muscles, or muscles about to die or greatly weakened by diseased conditions (§ 399). [The instantaneous induction-shock has a greater effect on the labile nerve than the slower less intense constant current. In the case of a muscle whose nerves are paralysed by curare an induction shock may fail to produce a contraction when applied to the muscle, but the constant current may do so. The induced shock must then be made much stronger in order to excite contraction. Sometimes in man, after paralysis of motor nerves, the constant current may excite contractions when the induced current fails. A strong constant current applied to a **curarised muscle** causes contraction not only at make and break, but during the passage of the current the muscle also remains contracted (p. 598). **Smooth muscle** is more readily excited by the constant current than by an induced shock.]

325. DIMINUTION OF THE EXCITABILITY.—DEGENERATION AND REGENERATION OF NERVES.—1. The **continuance of the normal excitability** in the nerves of the body **depends** upon the maintenance of the **normal nutrition** of the nerves themselves and a due supply of blood. Insufficient nutrition causes, in the first instance, increased excitability, and if the condition be continued the excitability is diminished (§ 339, I.).

When the physician meets with the *signs of increased excitability of the nerves*, under bad or abnormal conditions of nutrition, this is to be regarded as the beginning of the stage of decrease of the nerve-energy. Invigorating measures are required.

If the *terminal nervous apparatus* be subjected to a temporary disturbance of its nutrition, the return of the normal nutritive process is heralded by a more or less marked stage of excitement. The more excitable the nervous apparatus, the shorter must be the duration of the disturbance of nutrition, *e.g.*, cutting off the arterial blood-supply or interfering with the respiration.

2. **Fatigue of a Nerve.**—Continued **excessive stimulation** of a nerve, without sufficient intervals of repose, causes **fatigue** of the nerve, and by exhaustion rapidly diminishes the excitability. A nerve-trunk is more slowly fatigued than a muscle

(*Bernstein*), but it recovers more slowly (§ 304). [Nerves of cold-blooded animals (*Widenskii*) and mammals (*Bowditch*) may be tetanised for hours without becoming fatigued.]

[To show that a **muscle is much more rapidly fatigued than a nerve**, Bernstein arranged two nerve-muscle preparations so that both nerves were tetanised simultaneously, but through one of the nerves a polarising constant current was passed by means of non-polarisable electrodes (§ 328), so that the condition of anelectrotonus (§ 335) was set up in this nerve, and thus "blocked" the propagation of impulses to the corresponding muscle. Only one muscle, therefore, was tetanised. Both nerves were continuously stimulated until fatigue of the contracting muscle took place, and on breaking the polarising current applied to the other nerve, the corresponding muscle at once became tetanic. Now, as both nerves were equally stimulated, and the muscle in connection with one nerve was fatigued, while the other muscle at once contracted, it is evident that a muscle is much more rapidly fatigued than a motor nerve. In **sensory** nerves, fatigue and recovery are analogous to the corresponding processes in motor nerves (*Bernstein*).]

Recovery.—When a nerve recovers, at first it does so slowly, then more rapidly, and afterwards again more slowly. If recovery does not occur

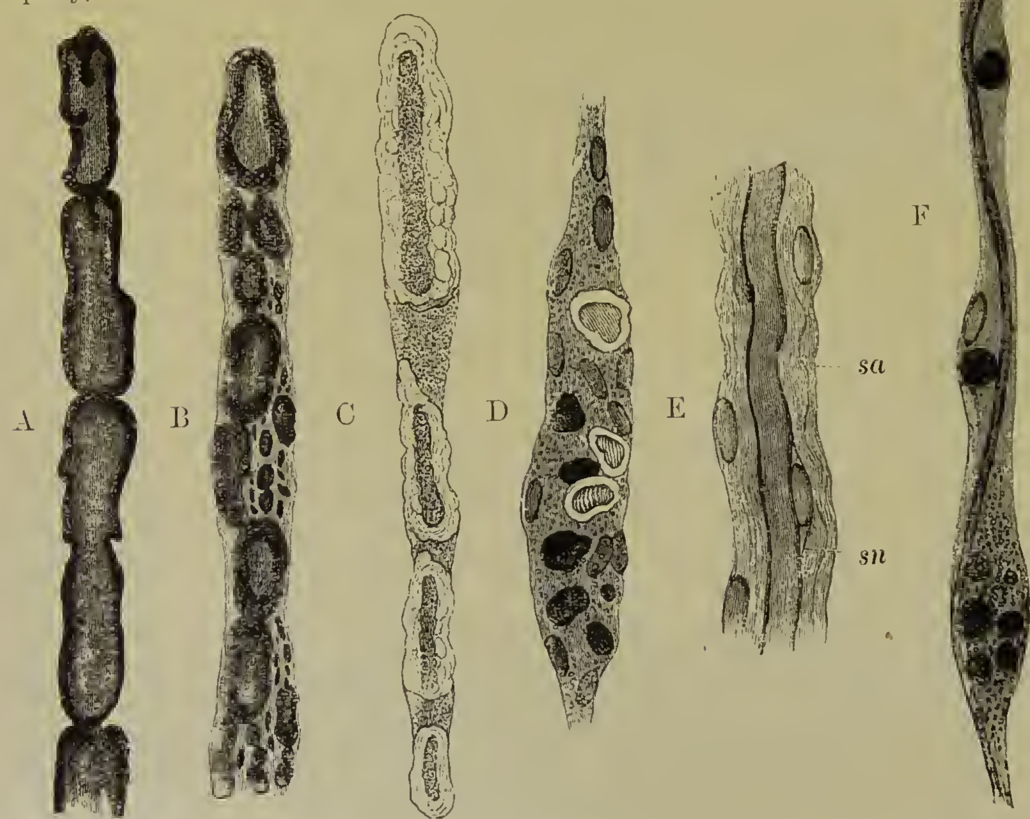


Fig. 456.

Degeneration and regeneration of nerves. A, sub-division of the myelin; B, further disintegration thereof (osmic acid staining); C, interruption of the axial cylinder, which is surrounded with the broken-up myelin; D, accumulation of nuclei, with the remainder of the myelin in a spindle-shaped fibre; E, a new nerve-fibre, with a new sheath of Schwann, *sn*, within the old sheath of Schwann, *sa*; F, a new nerve-fibre passing in a curved course through an old nerve-fibre sheath.

within half an hour after a frog's nerve has been subjected to very long and intense stimulation, it will not take place at all.

3. **Continued inaction** of a nerve diminishes, and may ultimately abolish the excitability.

Thus the central ends, *e.g.*, of a nerve of special sense, after removal of the sense-organ, or divided sensory nerves, after amputation of a limb, lose their excitability, although the nerves are still connected with the central nervous system, because the end-organs through which they were normally excited have been removed.

4. **Separation from their Nerve-Centres.**—The nerve-fibres remain in a condition of normal nutrition only when they are directly connected with their **centre**, which governs the **nutritive processes** within the nerve. If a nerve within the body be separated from its "**nutritive centre**" or "**trophic centre**"—either by section of the nerve or compressing it—within a short time it loses its excitability, and the *peripheral* end undergoes fatty degeneration, which begins in four to six days in warm-blooded animals, and after a long time in cold-blooded ones (*Joh. Müller*). See also the changes of the excitability during this condition, the so-called "**Reaction of degeneration**" (§ 339). If the *sensory* nerve-fibres of the root of a spinal nerve be divided on the central side of the ganglion, the fibres on the peripheral side do not degenerate, for the ganglion is the trophic or nutritive centre for the sensory nerves; but the fibres still in connection with the cord degenerate (*Waller*).

Wallerian Law of Degeneration.—Experiments on Spinal Nerves.—If a **spinal nerve** be divided, the peripheral part of the nerve and its branches, including the sensory and motor fibres, degenerate completely (fig. 457, A), while the central parts of the nerve remain unaltered. If the **anterior root** of a spinal nerve alone be divided before it joins the posterior root, all the peripheral nerve-fibres connected with the anterior root degenerate (fig. 457, B), so that in the nerve of distribution only the motor fibres degenerate. The portion of the nerve-root which remains attached to the cord does not degenerate. If the **posterior root** alone be divided, between the spinal cord and the ganglion, the effect is reversed, the part of the nerve-root lying between the section and the spinal cord degenerates, while the part of the nerve connected with the ganglion does not degenerate (fig. 457, C). The central fibres degenerate because they are separated

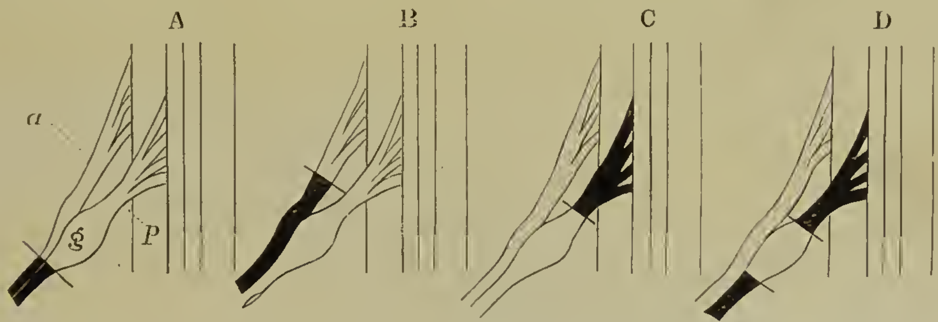


Fig. 457.

Diagram of the roots of a spinal nerve, showing the effect of section (the black parts represent the degenerated parts). A, section of the nerve-trunk beyond the ganglion; B, of the anterior root, and C, of the posterior; D, excision of the ganglion; *a*, anterior, *p*, posterior, root; *g*, ganglion.

from the ganglion. If the ganglion be excised, or if separated, as in fig. 457, D, both the central and peripheral parts of the posterior root degenerate. These experiments of Waller show that the fibres of the anterior and posterior roots are governed by different centres of nutrition or "**trophic centres.**" As the anterior root degenerates when it is separated from the cord, and the posterior when it is separated from its own ganglion, it is assumed that the trophic centre for the fibres of the anterior root lies in the multipolar nerve-cells of the anterior horn of the grey matter of the spinal cord, while that for the fibres of the posterior root lies in the cells of the ganglion placed on it. The nature of this supposed trophic influence is entirely unknown.]

Traumatic and Fatty Degeneration.—Both ends of the nerve at the point of section immediately begin to undergo "**traumatic degeneration.**" (In the frog on the 1st and 2nd day.) After a time neither the myelin nor axis-cylinder is distinguishable (*Schiff*). According to Engelmann, this condition extends only to the nearest node of Ranvier, and afterwards the so-called "**fatty degeneration**" begins. The process of "*fatty*" degeneration begins simultaneously in the whole peripheral portion; the white substance of Schwann breaks up into masses (fig. 456, A), just as it does after death, in microscopic preparations; afterwards the myelin forms globules and round masses (B), the axial-cylinder is compressed or constricted, and is ultimately broken across (C) in many places (7th day). The nerve-fibre seems to break up into two substances—one fatty, the other proteid in constitution, the fat being absorbed (*S. Mayer*). The nuclei of Schwann's sheath swell up and proliferate (D—until the 10th day). According to Ranvier, the nuclei of the interannular segments and their surrounding protoplasm proliferate, and ultimately interrupt the continuity of the axis-cylinder and the myelin. They then undergo considerable development with simultaneous disappearance of the medulla and axis-cylinder, or at least fatty substances formed by their degeneration, so that the nerve-fibres look like fibres of connective-tissue. [According to this view, the process is in part an *active* one, due to the growth of the nerve-corpuscles breaking up the contents of the neurilemma, which then ultimately undergo chemical degenerative changes.] According to Ranvier, Tizzoni, and others, leucocytes wander into the cut ends of the nerves, and also at Ranvier's nodes, insinuating themselves into the nerve-fibres, where they take myelin into their bodies, and subject it to certain changes. [These cells are best revealed by the action of osmic acid, which blackens any myelin particles in their interior.] Degeneration also takes place in the **motorial end-plates**, beginning first in the non-medullated branches, then in the terminal fibrils, and lastly in the nerve-trunks (*Gessler*).

Regeneration of Nerves.—In order that regeneration of a divided nerve may take place (*Cruickshank*, 1795), the divided ends of the nerve must be brought into contact (§ 244). In man this is done by means of sutures. About the middle of the fourth week, small clear bands appear within the neurilemma, winding between the nuclei and the remains of the myelin (E). They soon become wider, and receive myelin with incisures, and nodes, and a sheath of Schwann (2nd to 3rd month—F). The regeneration process takes place in each interannular segment, while the individual segments unite end to end at the nodes of Ranvier (§ 312, I., 5). On this view, each nerve-segment of the fibre corresponds to a "cell-unit" (*E. Neumann, Eichhorst*). The same process occurs in nerves *ligatured* in their course. *Several* new fibres may be formed within *one* old nerve-sheath. The divided axis-cylinders of the *central* end of the nerve begin to grow about the 14th day, until they meet the newly formed ones, with which they unite.

[**Primary and Secondary Nerve Suture.**—Numerous experiments on animals and man have established the fact that immediate or **primary suture** of a nerve, after it is divided, either accidentally or intentionally, hastens reunion and regeneration, and accelerates the restoration of function. **Secondary suture**, *i.e.*, bringing the ends together long after the nerve has been divided, has been practised with success. Surgeons have recorded cases where the function was restored after division had taken place for 3 to 16 months, and even longer, and in most cases the sensibility was restored first, the average time being 2 to 4 weeks. Motion is recovered much later. The ends of the nerve should be stitched to each other with catgut, the muscles at the same time being kept from becoming atrophied by electrical stimulation and the systematic use of massage (§ 307). After suture of a nerve, conductivity is restored in the rabbit in 40 days, on the 31st in dogs, and 25th in fowls, but after simple division without suture, not till the 60th day in the rabbit. **Transplantation of nerve** does not succeed (*Johnson*). It has been practised on several occasions on the human subject.]

Union of Nerves.—The central end of a divided motor nerve may unite with the peripheral end of another, and still conduct impulses (*Rava*). [It is stated that sensory fibres will reunite with sensory fibres, and motor fibres with motor fibres, and the regenerated nerve will, in the former case, conduct sensory impulses, and the latter motor impulses. There is very considerable diversity of opinion, however, as to the regeneration or union of sensory with motor fibres. Paul Bert made the following experiment:—He stitched the tail of a rat into the animal's back, and after union had taken place, he cut the tail from the body at the root, so that the tail, as it were, grew out of the animal's back, broad end uppermost. On irritating the end of the tail, which was formerly the root, the animal gave signs of pain. This experiment was devised by Bert to try to show that nerve-fibres can conduct impulses in both directions. One of two things must have occurred. Either the motor fibres, which normally carried impulses down the tail, now convey them in the opposite direction, and convey them to sensory fibres with which they have united; or the sensory fibres, which normally conducted impulses from the tip upwards, now carry them in the opposite direction. If the former were actually what happened, it would show that nerve-fibres of different function do unite (§ 349). Reichert asserts that he has succeeded in uniting the hypoglossal with the vagus in the dog. According to Gessler the end-plate is the first to regenerate (§ 338).]

Trophic Centres.—The regeneration of the nerve seems to take place under the influence of the **nerve-centres**, which act as their nutritive or trophic centres. Nerves permanently separated from these centres never regenerate.

During the **regeneration of a mixed nerve**, sensibility is restored first, subsequently voluntary motion, and lastly, the movements of the muscles, when their motor nerves are stimulated directly (*Schiff, Erb, v. Ziemssen*).

Wallerian Method of Investigation.—As the *peripheral* end of a nerve undergoes degeneration after section, we use this method for determining the course of nerve-fibres in a complex arrangement of nerves. The course of special nerve-fibres may be ascertained by tracing the degeneration tract (*Waller*). If after section, reunion or regeneration of a motor nerve does not take place, the muscle supplied by this nerve ultimately undergoes fatty degeneration.

5. **Modifying Conditions.**—Under the action of various operations, *e.g.*, *compressing* a nerve [so as not absolutely to sever the physiological continuity], it has been found that voluntary impulses or stimuli applied *above* the compressed spot give rise to impulses which are conducted through the nerve, and in the case of a motor nerve, cause contraction of the muscles, whilst the excitability of the parts *below* the injured spot is greatly diminished (*Schiff*). In a similar manner, it is found that the nerves of animals poisoned with CO_2, curare, or coniin, sometimes even the nerves of paralysed limbs in man, are not excitable to direct stimuli, while they are capable of conducting impressions coming from the central nervous system (*Duchenne*). The injured part of the nerve, therefore, loses its excitability sooner than its power of conducting an impulse.

6. Certain **poisons**, such as *veratrin*, at first increase the excitability of the nerves, and afterwards abolish it; with some other poisons, the abolition of the excitability passes off very rapidly, *e.g.*, curare. Conium, cynoglossum, iodide of methylstrychnin, and iodide of æthylstrychnin have a similar action.

If the nerve or muscle of a frog be placed in a solution of the poison, we obtain a different effect from that which results when the poison is injected into the body of the animal. Atropin diminishes the excitability of a nerve-muscle preparation of the frog without causing any previous increase, while alcohol, ether, and chloroform increase and then diminish the excitability (*Mommsen*).

7. **Ritter-Valli Law.**—If a nerve be separated from its centre, or if the centre die, the excitability of the nerve is *increased;* the increase of excitability begins at the central end, and travels towards the periphery—the excitability then *falls* until it disappears entirely. This process takes place more rapidly in the central than in the peripheral part of the nerve, so that the peripheral end of a nerve separated from its centre remains excitable for a longer time than the central end.

The **rapidity of the transmission** of **nerve impulses** in a nerve is increased when the excitability is increased, but it is lessened when the excitability is diminished (§ 337). In the latter condition, an electrical stimulus must last longer in order to be effective; hence rapid induction shocks may not produce any effect.

The *law of contraction* also undergoes some modification in the different stages of the changes of excitability (§ 336, II.).

8. **Excitable Points.**—Many nerves are more excitable at certain parts of their course than at others, and the excitability may last longer at these parts. One of these parts is the upper third of the sciatic nerve of a frog, just where a branch is given off (*Budge*).

The motor and sensory fibres of the upper third of the sciatic nerve of a frog (p. 662) are more excitable for all stimuli than the lower parts (*Grützner and Elpon*). Whether this arises from injury during preparation (a branch is given off there), or is due to anatomical conditions, *e.g.*, more connective-tissue and more nodes in the lower part of the sciatic, is undetermined (*Clara Halperson*).

This increased excitability may be due to injury to the nerve in preparing it for experiment. After section or compression of a nerve, all electrical currents employed to stimulate the nerve are far more active when the direction of the current passes away from the point of injury than

when they pass in the opposite direction. This is due to the fact that the current produced in the nerve after the lesion is added to the stimulation current (§ 331, 5). Even in intact nerves —sciatic of a frog—where the nerve ends at the periphery or at the centre, or where large branches are given off, there are points which behave in the same way as those points where a lesion has taken place (*Grützner and Moschner*).

Death of a Nerve.—In a dead nerve the excitability is entirely abolished, death taking place, according to the Ritter-Valli law, from the centre towards the periphery. The **reaction** of a dead nerve has been found by some observers to be acid (§ 322).

The functions of the **brain** cease immediately death takes place, while the vital functions of the **spinal cord**, especially of the white matter, last for a short time; the large **nerve-trunks** gradually die, then the nerves of the extensor muscles, those of the flexors after three to four hours; while the **sympathetic fibres** retain their excitability longest, those of the intestine even for ten hours (*Onimus*). Compare § 395. The nerves of a dead frog may remain excitable for several days, provided the animal be kept in a cool place.

Electro-Physiology.

Before beginning the study of electro-physiology, the student ought to read and study carefully the following short preliminary remarks on the **physics** of this question:—

326. **PHYSICAL—THE GALVANIC CURRENT—RHEOCORD.**—1. **Electro-motive Force.**—If two of the under-mentioned bodies be brought into direct contact, in one of them positive electricity, and, in the other, negative electricity can be detected. The cause of this phenomenon is the **electro-motive force.** The electro-motive substances may be arranged in a series of the **first class**, so that if the first-mentioned substance be brought into contact with any of the other bodies, the first substance is negatively, the last positively, electrified. This series is:—carbon, platinum, gold, silver, copper, iron, tin, lead, zinc, +.

The **Electro-motive Force** (E.M.F.) produced by the contact of two of these bodies is greater the further the bodies are apart in the series. The contact of the bodies may take place at one or more points. If several of the bodies of this series be arranged in a pile, the electrical tension thereby produced is just as great as if the two extreme bodies were brought into contact, the intermediate ones being left out.

2. The nature of the two electricities is readily determined by placing *one* of the bodies of the series in contact *with a fluid.* If zinc be placed in pure or acidulated water, the zinc is +(positive) and the water −(negative). If copper be taken instead of zinc, the copper is + but the fluid −. Experiment shows that those metals, in contact with fluid, are negatively electrified most strongly which are most acted on chemically by the fluid in which they are placed. Each such combination affords a constant difference of tension or potential. The tension [or power of overcoming resistance] of the amount of electricity obtained from both bodies depends upon the size of the surfaces in contact. The fluids, *e.g.*, the solutions of acids, alkalies, or salts are called exciters of electricity of the **second class.** They do not form among themselves a definite series with different tensions. When placed in these fluids, the metals lying next the + end of the above series, especially zinc, are most strongly electrified negatively, and to a less extent those lying nearer the − end of the series.

3. **Galvanic Battery.**—If two different exciters of the first class be placed in fluid, without the bodies coming into contact, *e.g.*, zinc and copper, the projecting end of the (negative) zinc shows free negative electricity, while the free end of the (positive) copper shows free positive electricity. Such a combination of two electro-motors of the first class with an electro-motor of the second class is called a *galvanic battery.* [A battery is an arrangement for producing electricity. A single apparatus constitutes a *cell* or *element*, several elements form a battery.] As long as the two metals in this fluid are kept separate, the circuit is said to be *broken* or *open*, but as soon as the free projecting ends of the metals are connected outside the fluid, *e.g.*, by a copper wire, the circuit or current is *made* or *closed*, and a **galvanic** or **constant current** of electricity is obtained. The galvanic current has resistance to encounter in its course, which is called "**conduction resistance**" (W). It is directly proportional—(1) to the **length** (l) of the circuit; (2) and with the same length of circuit, inversely as the **section** (q) of the same; and

(3) it also depends on the molecular properties of the conducting material (specific conduction resistance $= s$), so that—

$$\text{the conduction resistance } W = (s.\ l)\ :\ q.$$

The resistance to conduction increases with the increase of the temperature of the metals, but diminishes under similar conditions with fluids.

Ohm's Law.—The strength of a galvanic current (C), or the amount of electricity passing through the closed circuit, *i.e.*, the **current strength**, is proportional to the electro-motive force (E)—or the electrical tension or potential, but inversely proportional to the total resistance to conduction (R)—

$$\text{Ohm's Law (1827)} - \text{Current} = \frac{\text{Electro-motive force}}{\text{Total Resistance}}$$

$$C = \frac{E}{R} \text{ or } E = C \times R \text{ or } R = \frac{E}{C}$$

The total **resistance to conduction**, however, in a closed circuit is composed of (1) the resistance outside the battery ("extraordinary resistance"); and (2) the resistance within the battery itself ("essential resistance"). The specific resistance to conduction is very variable in different substances; it is relatively small in metals (*e.g.*, for copper $= 1$, iron $= 6{\cdot}4$, German silver $= 12$), but very great in fluids (*e.g.*, for a concentrated solution of common salt 6,515,000, for a concentrated solution of copper sulphate 10,963,600).

Conduction in Animal Tissues.—The resistance to the **conduction of electricity** is also very great in **animal tissues**, almost a million times greater than in metals. When a constant current is applied to the **skin** so as to traverse the body, the resistance diminishes because of the conduction of water in the epidermis under the action of the constant current (§ 289), and the congestion of the cutaneous blood-vessels in consequence of the stimulation. But the resistance varies in different parts of the skin, the least being in the palm of the hand and sole of the foot. The chief seat of the resistance is the epidermis, for after its removal by means of a blister, the resistance is greatly diminished. Dead tissue, as a rule, is a worse conductor than living tissues (*Jolly*). When the current is passed *transversely* to the direction of the fibres of a **muscle**, the resistance is nearly nine times as great as when the current passes in the direction of the fibres—a condition which disappears in rigor mortis (*Hermann*). In **nerves**, the resistance longitudinally is two and a half million times greater than in mercury, transversely about twelve million times greater (*Hermann*). Tetanus and rigor mortis diminish the resistance in muscle (*du Bois-Reymond*). According to Rosenthal, the conduction is the same in a dead as in a living muscle, both in a longitudinal and transverse direction. Charcot and Vigouroux have made the remarkable observation that in cases of Basedow's disease (§ 371) there is a diminution of the electrical resistance in the body.

Deductions from Ohm's Law.—It follows from Ohm's law that—**I.** If there is very great resistance to the current outside the battery [*i.e.*, between the electrodes], as is the case when a nerve or a muscle lies on the electrodes, the strength of the current can only be increased by increasing the number of the electro-motive elements. **II.** When, however, the extraordinary resistance is very small compared with that within the battery itself, the strength of the current cannot be increased by increasing the number of the elements, but only by increasing the surfaces of the plates in the battery.

[The following system of electrical measurements was adopted in 1881. Some of the units of measurement are of importance physiologically. They are:—

The Ohm, or the **unit resistance**, is equal to the resistance of a column of pure mercury in a closed glass tube 1·06 metre long, and 1 square mm. in sectional area at 0° C.

The Ampère, or the **unit of current**, is the strength of current required to produce 0·172 c.c. of O and H (*i.e.*, decompose water) in 1 sec. at 0° C. and 760 mm. pressure. 1 milliampère $= \frac{1}{1000}$ ampère. An ampère is approximately equal to the current of a Daniell's cell through an ohm.

The **Volt**, or **unit electromotive force**, is equal to about E.M.F. of a Daniell's cell. The relation between these is that 1 ampère $=$ 1 volt : 1 ohm.]

Strength and Intensity.—We must carefully distinguish the **strength** of the current from its **intensity**. As the same amount of electricity always flows through any given transverse section of the circuit, then, if the size of the transverse section of the circuit varies, the electricity must be of greater intensity in the narrower parts, and it is evident that the intensity will be less where the transverse section is greater. Let $C =$ the strength of the current, and q the transverse section of the given part of the circuit, then the intensity (d) at the latter part is $d = C : q$.

If the galvanic current passing from the positive pole of a battery is divided into two or more streams, which are again reunited at the other pole, then the sum of the strength of all the streams is equal to the strength of the undivided stream. If, however, the different streams are different as regards length, section, and material, then the strength of the current passing in each of the streams is inversely proportional to the resistance to the conduction.

Du Bois-Reymond's Rheocord.—This instrument, constructed on the principle of the "secondary," or "**short circuit**," enables us to **graduate the strength of a galvanic current** to any required degree, for the stimulation of nerve and muscle. From the two poles (fig. 458, *a*, *b*) of a constant battery, there are two conducting wires (*a*, *c*, and *d*, *b*), which go to the nerve of a frog's nerve-muscle preparation (F). The portion of nerve (*c*, *d*) introduced into this circuit (*a*, *c*, *d*, *b*) offers *very great* resistance. The second stream or secondary circuit (*a* A, *b* B) conducted from *a* and *b* passes through a thick brass plate (A, B), consisting of seven pieces of brass (1 to 7) placed end to end, but not in contact. They can all, with the exception of 1 and 2, be made to form a continuous conductor by placing in the spaces between them the brass plugs (S_1 to S_5). Evidently, with the arrangement shown in fig. 458, only a minimal part of the current will pass through the nerve (*c*, *d*), owing to the very great resistance in it, while by far the greatest part will pass through the good conducting medium of brass (A, L, B). If new **resistance** be introduced into this circuit, then the *a*, *c*, *d*, *b* stream will be strengthened. This

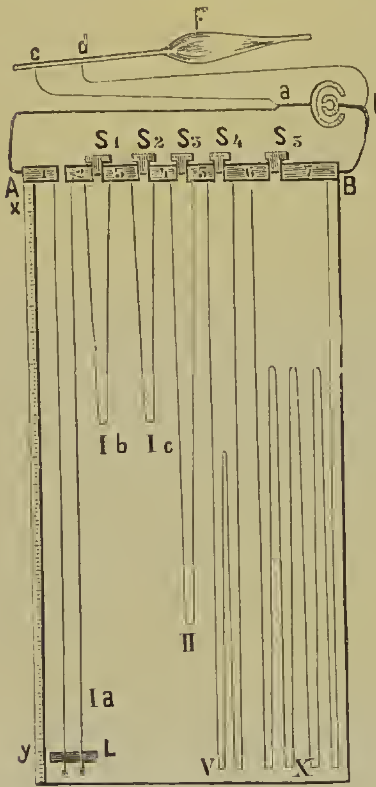


Fig. 458.

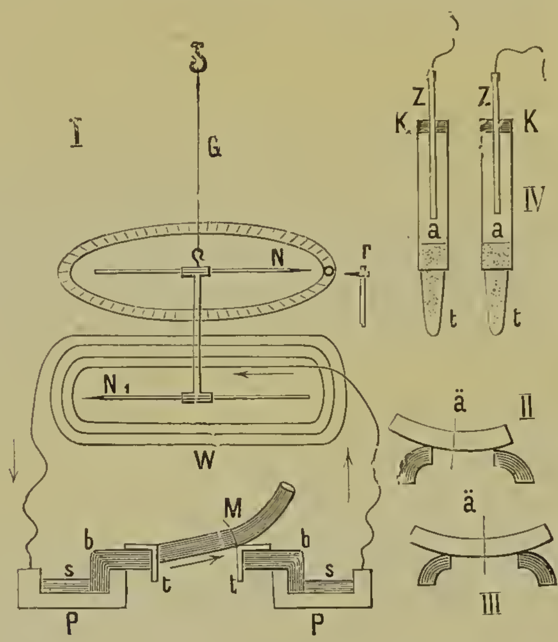


Fig. 459.

Fig. 458.—Scheme of du Bois-Reymond's rheocord. Fig. 459.—Scheme of the galvanometer. N, N, astatic needles suspended by the silk fibre, G; P, P, nonpolarisable electrodes, containing zinc sulphate solution, *s*, and pads of blotting-paper, *b*, covered with clay, *t*, *t*, on which the muscle, M, is placed; II and III, arrangement of the muscle on the electrodes; IV, non-polarisable electrodes; Z, zinc wire; K, cork; *a*, zinc sulphate solution; *t*, *t*, clay points.

resistance can be introduced into the latter circuit by means of the thin wires marked I *a*, I *b*, I *c*, II, V, X. Suppose all the brass plugs from S_1 to S_5 to be removed, then the current entering at A must traverse the whole system of thin wires. Thus, there is more resistance to the passage of this current, so that the current through the nerve must be strengthened. If only one brass plug be taken out, then the current passes through only the corresponding length of wire. The resistances offered by the different lengths of wire from I *a* to X are so arranged that I *a*, I *b*, and I *c* each represents a unit of resistance; II, double; V, five times; and X, ten times the resistance. The length of wire, I *a*, can also be shortened by the movable **bridge** (L) [composed of a small tube filled with mercury, through which the wires pass], the scale (*x*, *y*) indicating the length of the resistance wires. It is evident that, by means of the bridge, and by the method of using the brass plugs, the apparatus can be graduated to yield very variable currents for stimulating nerve or muscle. When the bridge (L) is pushed hard up to 1 and 2, the current passes directly from A to B, and not through the thin wires (I *a*).

The **rheostat** is another instrument used to vary the resistance of a galvanic current (*Wheatstone*).

327. ACTION OF THE GALVANIC CURRENT ON A MAGNETIC NEEDLE—GALVANOMETER—In 1822, Oersted of Copenhagen found that a magnetic needle, suspended in the magnetic meridian, was deflected by a constant current of electricity passed along a wire parallel to it. [The side to which the north pole is deflected depends upon the direction of the current, and whether it passes above or below the needle.]

Ampère's Rule.—Ampère has given a simple rule for determining the direction. If an observer be placed parallel to and facing the needle, and if the current be passing from his feet to his head, then the north pole of the needle will always be deflected to the *left,* and the south pole in the opposite direction. The effect exerted by the constant current acts always in a direction towards the so-called electro-magnetic plane. The latter is the plane passing through the north pole of the needle, and two points in the straight wire running parallel with the needle. The force of the constant current, which causes the deflection of the magnetic needle, is proportional to the sine of the angle between the electro-magnetic plane and the plane of vibration of the needle.

Multiplicator or **Galvanometer.**—The deflection of the needle caused by the constant current may be increased by coiling the conducting wire *many* times in the same direction on a rectangular frame, or merely around and in the same direction as the needle [provided that each turn of the wire be properly insulated from the other]. An instrument constructed on this principle is called a multiplicator, multiplier, or **galvanometer.** The greater the number of turns of the wire the greater is the angle of deflection of the needle, although the deflection is not directly proportional, as the several turns or coils are not at the same distance from, or in the same position as, the needle. By means of the multiplier we may detect the presence [and also the amount and direction] of *feeble currents.* Experience has shown that, when great resistance (as in animal tissues) is opposed to the weak galvanic currents, we must use a very large number of turns of thin wire round the needle. If, however, the resistance in the circuit is but small, *e.g.*, in thermo-electrical arrangements, a few turns of a *thick* wire round the needle are sufficient. The multiplier may be made more sensitive by *weakening the magnetic directive force of the needle,* which keeps it pointing to the north.

Galvanometer and Astatic Needles.—In the multiplier of Schweigger, used for physiological purposes, the tendency of the needle to point to the north is greatly weakened by using the **astatic needles** of Nobili. [A multiplier of galvanomotor with a single magnetic needle always requires comparatively strong currents to deflect the needle. The needle is continually acted upon by the directive magnetic influence of the earth, which tends to keep it in the magnetic meridian, and, as soon as it is moved out of the magnetic meridian, the directive action of the earth tends to bring it back. Hence, such a simple form of galvanometer is not sufficiently sensitive for detecting feeble currents. In 1827, Nobili devised an astatic combination of needles, whereby the action of the earth's magnetism was diminished.] Two similar magnetic needles are united by a solid light piece of horn [or tortoise shell], and are so arranged that the north pole of the one is placed over or opposite to the south pole of the other (fig. 459).

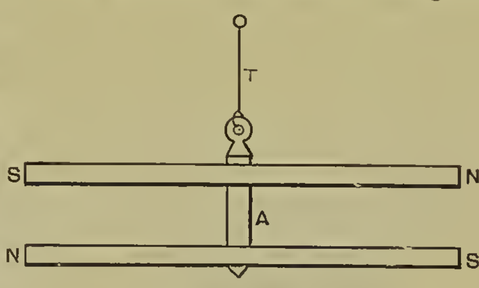


Fig. 460.
Astatic needles.

[Fig. 460 shows two magnetic needles with their magnetic axes parallel and their similar poles pointing opposite ways, forming what is called an **astatic pair,** or **astatic needles.** As the earth's attractive force on the N. pole of one needle is exactly counterbalanced by its repelling force on the S. pole of the other needle, there is no directive force to cause the combination to set in any particular position.]

[If both needles are equally magnetised, then the earth's influence on the needle is neutralised, so that the needles no longer adjust themselves in the magnetic meridian; hence, such a system is called **astatic** (*statum,* standing).] As it is impossible to make both needles of absolutely equal magnetic strength, one needle is always stronger than the other. The difference, however, must not be so great that the stronger needle points to the north, but only that the freely suspended system of needles forms a certain angle with the magnetic meridian, into which position the system always swings after it is deflected from this position. This angular deviation of the astatic system towards the magnetic meridian is called the "**free deviation.**" The more perfectly an astatic condition is reached, the nearer does the angle formed by the direction of the free deviation with the magnetic meridian become a right angle. The greater, therefore, the astatic condition, the fewer vibrations will the astatic system make in a given time, after it has been deflected from its position. The duration of each single vibration is also very great. [Hence, when using a galvanometer, and adjusting its needle to zero, if the magnets dance about or move quickly, then the system is not sensitive, but a sensitive condition of the needles is indicated by a *slow* period of oscillation.]

In making a galvanometer, the turns of the wire must have the same direction as the needles.

In Nobili's galvanometer, as improved by du Bois-Reymond, the upper needle swings above a card divided into degrees (fig. 459), on which the extent of its deflection may be read off. Even the purest copper wire used for the coils round the needles always contains a trace of iron, which exerts an influence upon the needles. Hence, a small fixed directive or compensatory magnet (r) is placed near one of the poles of the upper needle to compensate for the action of the iron on the needles.

328. **ELECTROLYSIS, POLARISATION, BATTERIES.—Electrolysis.**—Every galvanic current which traverses a fluid conductor causes decomposition or electrolysis of the fluid. The decomposition-products, called "**ions**," accumulate at the **poles (electrodes)** in the fluid, the positive pole (+) being called the **anode** [ἀνά, up, ὁδὸς, a way], the negative pole (−) the **cathode** (κατά, down, ὁδὸς, a way). The **anions** accumulate at the anode and the **kations** at the cathode.

Transition Resistance.—When the decomposition-products accumulate upon the electrodes, by their presence they either increase or diminish the resistance to the electrical current. This is called *transition resistance*. If the resistance within the battery is thereby increased, the transition resistance is said to be *positive;* if diminished, *negative*.

Galvanic Polarisation.—The ions accumulated on the electrodes may also vary the strength of the current, by developing between the anions and kations a new galvanic current, just as occurs between two different bodies connected by a fluid medium. This phenomenon is called **galvanic polarisation.** Thus, when water is decomposed, the electrodes being of platinum, the oxygen (negative) accumulates at the + pole, and the hydrogen (positive) at the − pole. Usually the polarisation current has a direction *opposite* to the original current; hence, we speak of **negative polarisation.** When the two currents have the same direction, **positive polarisation** obtains. Of course, transition resistance and polarisation may occur together during electrolysis.

Test of polarisation.—Polarisation, when present, may be so slight as not to be visible to the eye, but it may be detected thus:—After a time exclude the primary source of the current, especially the element connected with the electrodes, and place the free projecting end of the electrodes in connection with a galvanometer, which will at once indicate, by the deflection of its needle, the presence of even the slightest polarisation. [**Polarisation of Electrodes.**—By means of copper electrodes, pass a constant current of electricity through a nerve of a nerve-muscle preparation, introducing a key in the circuit. After three minutes remove the battery, and open and close the key; on doing so the muscle will contract owing to polarisation of the electrodes.]

Secondary decompositions.—The ions excreted during electrolysis cause, especially at their moment of formation, secondary decompositions. With platinum electrodes in a solution of common salt, chlorine accumulates at the anode and sodium at the cathode; but the latter at once decomposes the water, and uses the oxygen of the water to oxidise itself, while the hydrogen is deposited secondarily upon the cathode. The amount of polarisation increases, although only to a slight extent, with the *strength of the current*, while it is nearly proportional to the *increase of the temperature*.

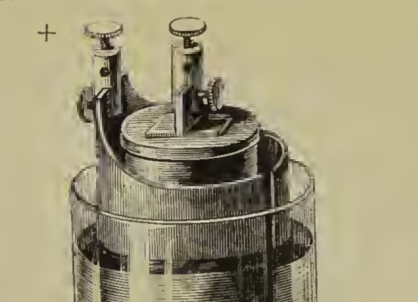


Fig. 461.
Large Grove's cell.

Non-polarisable electrodes.—The attempts to get rid of polarisation, which obviously must very soon alter the strength of the galvanic current, have led to the discovery of two important arrangements, viz., the construction of **constant galvanic batteries**, and **non-polarisable electrodes** (*du Bois-Reymond*).

Constant Batteries, Elements, or Cells.—A perfectly constant element produces a **constant current**, *i.e.*, one remaining of equal strength, by the ions produced by the electrodes being got rid of the moment they are formed, so that they cannot give rise to polarisation. For this purpose, each of the substances from the tension series used is placed in a special fluid (§ 326), both fluids being separated by a porous septum (porcelain cylinder).

Grove's cell, or **platinum-zinc cells**, has two metals and two fluids (figs. 461, 462, 463). The zinc is in the form of a roll placed in dilute sulphuric acid [1 acid to 7 of water, which is contained in a glass, porcelain, or ebonite vessel]. The platinum is in contact with strong nitric acid, [which is contained in a porous cell placed inside the roll of zinc.] The O, formed by the electrolysis and deposited on the zinc plate,

forms zinc oxide, which is at once dissolved by the sulphuric acid. The hydrogen on the platinum unites at once with the nitric acid, which gives up O and forms nitrous acid and water, thus—

$$[H_2 + HNO_3 = HNO_2 + H_2O.]$$

[Platinum is the + pole, and zinc the − .]

[Grove's battery is very powerful, but the nitrous fumes are very disagreeable and irritating; hence these elements should be kept in a special well-ventilated recess in the laboratory, in an evaporating chamber, or under glass. The fumes also attack instruments. The E.M.F. is about 2 volts.]

The zinc plate in this battery is generally cast in the form of a U and is generally placed in an ebonite vessel (EV) (fig. 463).

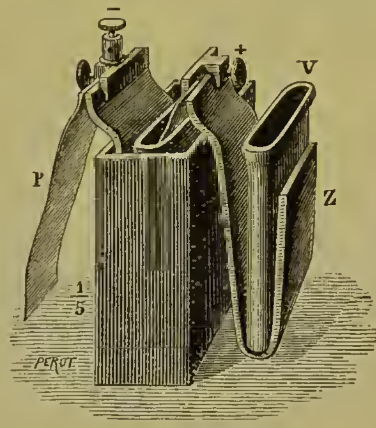


Fig. 462.

Outside view of a Grove's cell, showing platinum (P) and zinc plates (Z) as well as porous pot (V) of next cell in series.

Bunsen's cell, or **carbon-zinc cell** (fig. 464), is similar to Grove's, only a piece of compressed carbon is substituted for the platinum in contact with the nitric acid. The E.M.F. = 1·9 volt.

[The carbon is the + pole, the zinc the − .]

[**Daniell's cell** consists of an outer vessel of glass or earthenware, and sometimes of metallic copper, filled with a saturated solution of cupric sulphate (fig. 465). A roll of copper, perforated with a few holes, is placed in the copper solution, and in order that the latter be kept *saturated*, and to supply the place of the copper used up by the battery when in action, there is a small shelf on the copper roll, on which are placed crystals of cupric sulphate. A porous earthenware vessel containing zinc in contact with dilute sulphuric acid (1 : 7) is placed within the copper cylinder. When the circuit is completed, the zinc is acted on, zinc sulphate being formed, and hydrogen liberated. The hydrogen *in statu nascendi* passes through the porous cell, reduces the cupric sulphate to metallic copper, which is precipitated on the copper cylinder, so that the latter is always kept bright and clean. The liberated sulphuric acid replaces that in contact with the zinc. Owing

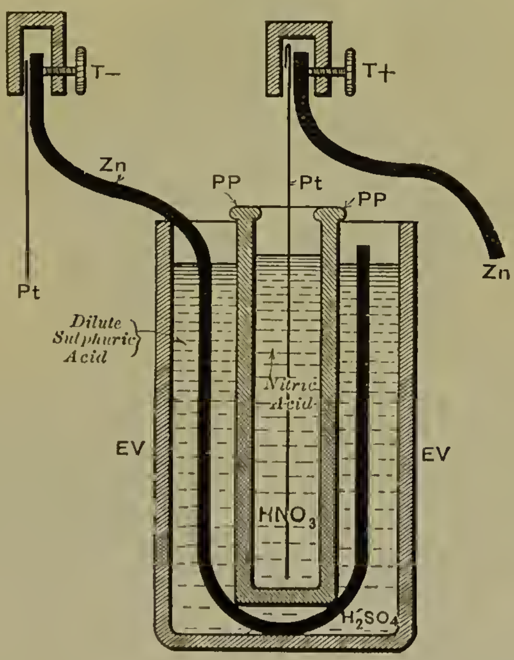


Fig. 463.

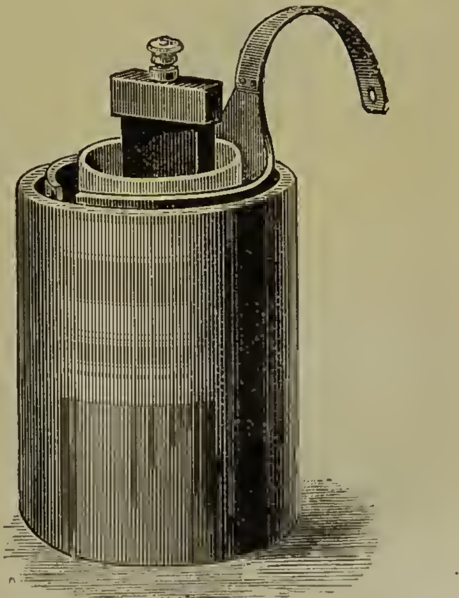


Fig. 464.

Fig. 463.—Vertical section through a Grove's cell; *p*, porous pot; EV, ebonite vessel.
Fig. 464.—Outside view of a Bunsen cell.

to the absence of polarisation, the Daniell is one of the most constant batteries, and is generally taken as the standard of comparison. The E.M.F = 1·072 volt.

[The copper is the + pole, and zinc the − .]

[**Smee's cell** contains only one fluid, viz., dilute sulphuric acid (1 : 7), in which the two metals, zinc and platinum, or zinc and platinised silver, are placed. The E.M.F. = ·47 volt.

The platinum is the + pole, and zinc the − .]

[**Grennet's or the Bichromate cell** consists of one plate of zinc and two plates of compressed carbon in a fluid, containing bichromate of potash, sulphuric acid, and water. The fluid consists of 1 part of potassium bichromate dissolved in 8 parts of water, to which one part of sulphuric acid is added. Measure by *weight*. The cell consists of a wide-mouthed glass bottle (fig. 466); the carbons remain in the fluid, while the zinc can be raised or depressed. When not in action, the zinc, which is attached to a rod (B), is lifted out of the fluid. It is not a very constant battery. When in action, the zinc is acted on by the sulphuric acid, hydrogen being liberated, which reduces the bichromate of potash. The E.M.F. = 1·8 volt.

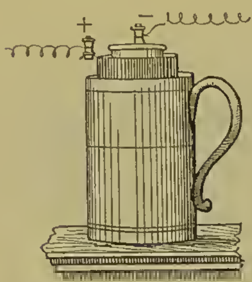


Fig. 465.
Daniell's cell.

The carbon is the + pole, and the zinc the − .]

[**Leclanché's cell** (fig. 467) consists of an outer glass vessel containing zinc in a solution of ammonium chloride, while the porous cell contains compressed carbon in a fluid mixture of black oxide of manganese and carbon. It is most frequently used for electric bells, as its feeble current lasts for a long time. The E.M.F. = 1·48 volt.

The carbon is the + pole, and the zinc the − .]

[**Noë-Dörffel thermo-electric battery.**—This consists of a number of thermo-electric junctions of German silver and an alloy of antimony and zinc arranged concentrically. The apparatus is heated by means of a gas flame or a Bunsen burner. Twenty elements in a battery

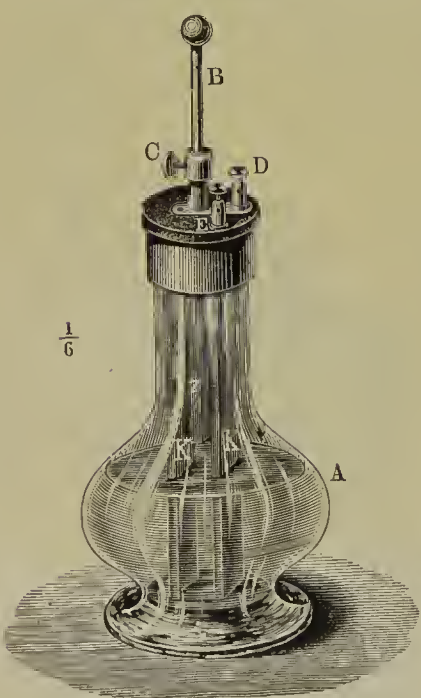


Fig. 466

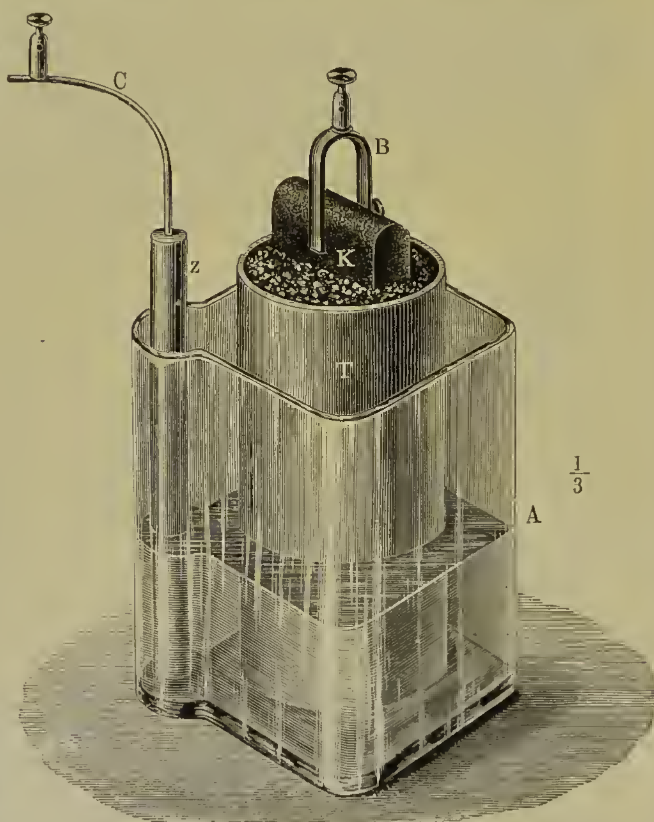


Fig. 467

Fig. 466.—Grennet's cell. A, glass vessel; K, K, carbon; Z, zinc; D, E, binding screws for the wires; B, rod to raise the zinc from the fluid; C, screw to fix B. Fig. 467.—Leclanché's cell. A, outer vessel; T, porous cylinder, containing K, carbon; B, binding screw; Z, zinc; C, binding screw of negative pole.

give a current equal to about 1·25 volts. The − pole is connected with the German silver.]

[**Storage cell.**—If a dynamo be available storage cells may be used. They require to be changed from time to time from the dynamo.]

[The kind of electricity yielded by all these batteries is spoken of as the **constant current**, or **voltaic**, or **galvanic electricity.**]

[When a number of cells are used, and it is desired to obtain a strong current of electricity, the cells are joined in **series** (fig. 468), *i.e.*, the positive terminal of one cell is joined to the negative of the next, and so on. A current of higher potential is obtained if several elements of small size are used, but if a large quantity of electricity is required, as for thermo-cautery, use elements of large size.]

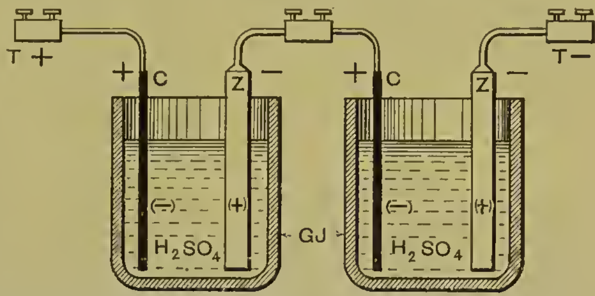


Fig. 468.
Two simple voltaic cells joined in series. C, copper Z, zinc.

Non-polarisable Electrodes. — If a constant current be applied to moist animal tissues, *e.g.*, nerve or muscle, by means of ordinary electrodes composed either of copper or platinum, of course electrolysis must occur, and in consequence thereof polarisation takes place (p. 672). In order to avoid this, non-polarisable electrodes (figs. 459, 469) are used. Such electrodes are made by taking two pieces of carefully amalgamated, pure **zinc wire** (*z*, *z*), and dipping these in a **saturated solution of zinc sulphate** contained in tubes (*a*, *a*), whose lower ends are closed by means of modeller's **clay** (*t*, *t*), moistened with 0·6 per cent. normal saline solution or water. The contact of the tissues with these electrodes does not give rise to polarity. [The **brush electrodes** of v. Fleischl are very serviceable (fig. 470). The lower end of the glass tube is plugged with a camel-hair pencil, moistened with modeller's clay, otherwise the arrangement is the same as shown in fig. 459, IV.]

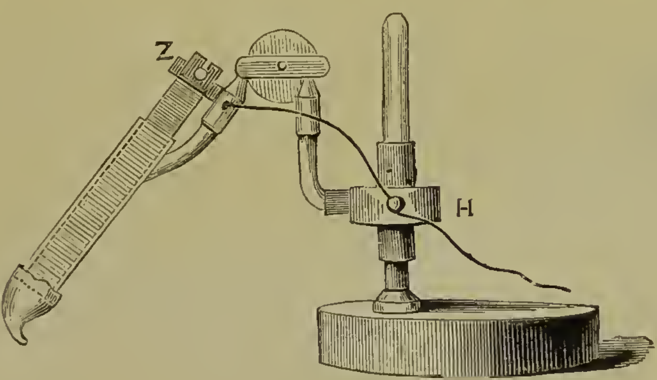


Fig. 469.

Fig. 470.

Fig. 469.—Non-polarisable electrode of du Bois-Reymond. Z, zinc ; H, movable support ; C, clay point—the whole on a universal joint. Fig. 470.—Brush electrodes of v. Fleischl.

Arrangement for the Muscle- or Nerve-Current.—In order to investigate the **electrical currents of nerve or muscle**, the tissue must be placed on **non-polarisable electrodes**, which may either be one of the forms described above or the original form used by du Bois-Reymond (fig. 459). The last consists of two zinc troughs (*p*,*p*), thoroughly amalgamated inside, insulated on vulcanite, and filled with a saturated solution of zinc sulphate (*s*, *s*). In each trough is placed a thick pad or cushion of white blotting-paper (*b*, *b*) saturated with the same fluid [**deriving cushions**]. [The cushion consists of many layers, almost sufficient to fill the trough, and they are kept together by a thread. To prevent the action of the zinc sulphate upon the tissue, each cushion is covered with a thin layer of modeller's clay (*t*, *t*), moistened with 0·6 per cent. saline solution, which is a good conductor [**clay guard**]. The clay guard prevents the action of the solution upon the tissue. Connected with the electrodes are a pair of binding screws whereby the apparatus is connected with the galvanometer (fig. 459).

[**Reflecting Galvanometer.**—The form of galvanometer, used in this country for physiological purposes, is that of Sir William Thomson (fig. 471). In Germany, Wiedemann's form is more commonly used. In Thomson's instrument, the **astatic needles** are very light, and connected to each other by a piece of aluminium, and each set of needles is surrounded by a separate coil of wire, the lower coil (*l*) winding in a direction opposite to that of the upper (*u*). A small, round, light, slightly **concave mirror** is fixed to the upper set of needles. The needles are sus-

pended by a delicate silk fibril, and they can be raised or lowered as required by means of a small milled head. When the milled head is raised, the system of needles swings freely. The coils are protected by a glass shade, and the whole stands on a vulcanite base, which is levelled by three screws (*s*, *s*). On a brass rod (*b*) is a feeble magnet (*m*), which is used to give an artificial meridian. The magnet (*m*) can be raised or lowered by means of a milled head.]

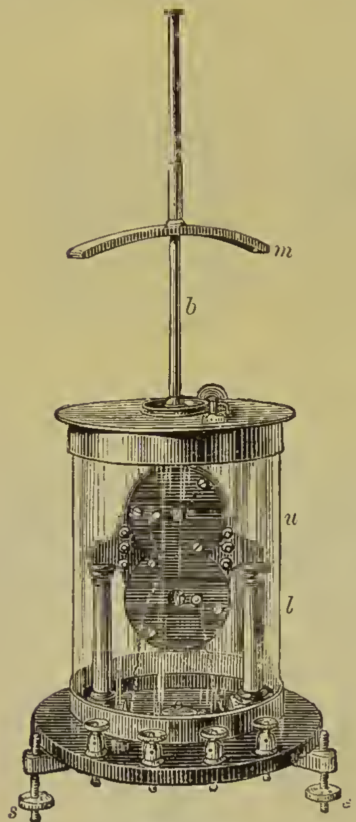


Fig. 471.

Thomson's reflecting galvanometer. *u*, upper, *l*, lower coil; *s*, *s*, levelling screws; *m*, magnet, on a brass support, *b*.

[**Lamp and Scale.**—When the instrument is to be used, place it so that the coils face east and west. At 3 feet distant from the front of the galvanometer, facing west, is placed the lamp and scale (fig. 472). There is a small vertical slit in front of the lamp, and the image of this slit is projected on the mirror attached to the upper needles, and by it is reflected on to the paper scale fixed just above the slit. The spot of light is focussed at zero by means of the magnet, *m*. The needles are most sensitive when the oscillations occur slowly. The sensitiveness of the needles can be regulated by means of the magnet. In every case the instrument must be quite level, and for this purpose there is a small spirit-level in the base of the galvanometer.]

[**Shunt.**—As the galvanometer is very delicate, it is convenient to have a shunt to regulate to a certain extent the amount of electricity transmitted through the galvanometer (fig. 473). The shunt consists of a brass box containing coils of German silver wire, and is constructed on the same principle as resistance coils of the rheocord (§ 326). On the upper surface of the box are several plates of brass separated from each other, like those of the rheocord, but which can be united by brass plugs. The two wires coming from the electrodes are connected with the two binding screws, and from the latter two wires are led to the outer two binding screws of the galvanometer. By placing a plug between the brass plates attached to the two binding screws in the figure, the current is short-circuited. On removing both plugs, the whole of the current must pass through the galvanometer. If *one* plug be placed between the central disc of brass and the plate marked $\frac{1}{9}$, (the other being left out), then $\frac{1}{10}$ of the current goes through the galvanometer and $\frac{9}{10}$th to the electrodes. If the plug be placed as shown in the figure opposite $\frac{1}{99}$ then $\frac{1}{100}$th of the current goes to the galvanometer, while $\frac{99}{100}$ths are short-circuited. If the plug be placed opposite $\frac{1}{999}$, only $\frac{1}{1000}$th part goes through the galvanometer.]

Internal Polarisation of Moist Bodies.—Nerves and muscular fibres, the juicy parts of vegetables and animals, fibrin, and other similar bodies possessing a porous structure filled with fluid, exhibit the phenomena of polarisation when subjected to strong currents—a condition termed internal polarisation of moist bodies by du Bois-Reymond. It is assumed that the solid parts in the interior of these bodies which are better conductors produce electrolysis of the adjoining fluid, just like metals in contact with fluid. The ions produced by the decomposition of the internal fluids give rise to differences of potential, and thus cause internal polarisation (§ 333).

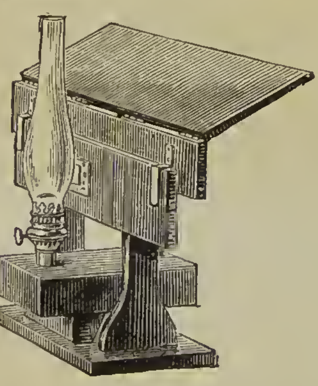


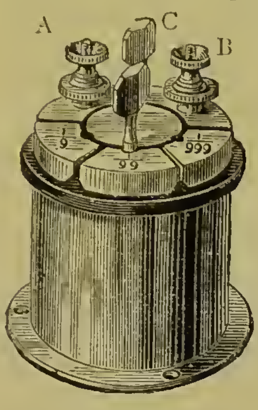
Fig. 472.

Lamp and scale for Thomson's galvanometer.

Cataphoric Action.—If the two electrodes from a galvanic battery be placed in the two compartments of a fluid, separated from each other by a porous septum, we observe that the fluid particles pass in the direction of the galvanic current, from the + to the − pole, so that after some time, the fluid in the one half of the vessel increases, while it diminishes in the other. The phenomena of direct transference were called by du Bois-Reymond the *cataphoric action of the constant current.* The introduction of dissolved substances through the skin by means of a constant current depends upon this action (§ 289), and so does the so-called **Porret's phenomenon** in living muscle (§ 293, 1, *b*).

External Secondary Resistance.—This condition also depends on cataphoric action. If the copper electrodes of a constant battery be placed in a vessel filled with a solution of cupric

sulphate, and from each electrode there project a cushion saturated with this fluid, then, on placing a piece of muscle, cartilage, vegetable tissue, or even a prismatic strip of coagulated albumin across these cushions, we observe that, very soon after the circuit is closed, there is a considerable variation of the current. If the direction of the current be reversed, it first becomes stronger, but afterwards diminishes. By constantly altering the direction of the current we cause the same changes in the intensity. If a prismatic strip of coagulated albumin be used for the experiment, we observe that, simultaneously with the enfeeblement of the current in the neighbourhood of the + pole, the albumin loses water and becomes more shrivelled, while at the – pole the albumin is swollen up and contains more water. If the direction of the current be altered, the phenomena



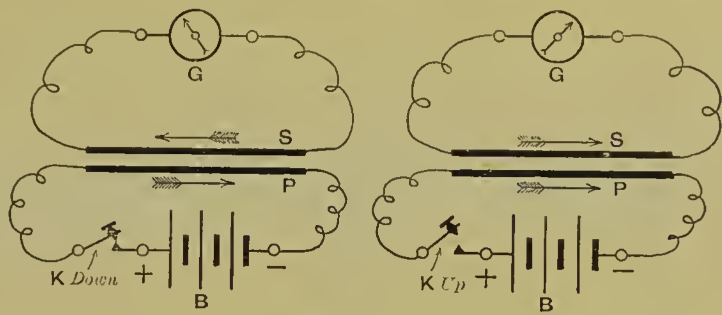


Fig. 473. Fig. 474.

Fig. 473.—Shunt for galvanometer. Fig. 474.—Induced currents in straight parallel closed circuits. B, battery; K, key; P, S, primary and secondary circuits; G, galvanometer.

are also changed. The shrivelling and removal of water in the albumin at the positive pole must be the cause of the resistance in the circuit which explains the enfeeblement of the galvanic current. This phenomenon is called "external secondary resistance" (*du Bois-Reymond*).

[**Induced currents in a closed secondary circuit.**—Suppose the parallel straight wires to be joined up, as shown in fig. 474. (1) Close the primary circuit (P), by putting down the key (K). A momentary current is induced in the *opposite direction* in the secondary circuit (S). (2) Suddenly increase the current by switching in one or more cells, and again a momentary *inverse current* is observed in the secondary. (3) Break the current in the primary coil by raising the key (K). A momentary *direct current, i.e.*, one in the same direction, is induced in the secondary circuit; and (4) the same result is obtained by suddenly diminishing the current in the primary (by switching out one or more cells).

Precisely the same results are obtained with two closed spirals or selenoidal coils of wire, only the induced currents will be stronger; and the effects will be made still stronger by putting a piece of soft iron into the heart of each coil.

Table of Induction Currents (*Jamieson*).

Momentary **inverse** currents are induced in a secondary circuit	Momentary **direct** currents are induced in a secondary circuit
By (1) *Approach* to primary. ,, (2) *Starting* primary current. ,, (3) *Increasing* primary current.	By (1) *Withdrawal* from primary. ,, (2) *Stopping* primary current. ,, (3) *Decreasing* primary current.]

329. **INDUCTION—EXTRA-CURRENT—MAGNETIC-INDUCTION.—Induction of the Extra-Current.**—If a galvanic element is closed by means of a short arc of wire, at the moment the circuit is again opened or broken, a *slight* spark is observed. If, however, the circuit is made or closed by means of a very long wire rolled in a coil, then on breaking the circuit there is a *strong* spark. If the wires be connected with two electrodes, so that a person can hold one in each hand, the current at the moment it is opened must pass through the person's body, then there is a violent shock communicated to the hand. This phenomenon is due to a current induced in the long spiral of wire which Faraday called the **extra-current.** It is caused thus:—When the circuit is closed by means of the spiral wire, the galvanic current passing along it excites or induces an electric current in the adjoining coils of the same spiral. At the moment of closing or making the circuit in the spiral, the induced current is in the opposite direction to the galvanic current in the circuit; hence its strength is lessened, and it causes no shock.

At the moment of opening, however, the induced current has the same direction as the galvanic stream, and hence its action is strengthened.

Magnetisation of Iron by the Galvanic Current.—If a rod of soft iron be placed in the cavity of a spiral of copper wire, then the soft iron remains magnetic as long as a galvanic current circulates in the spiral. If one end of the iron rod be directed towards the observer, and the other away from him, and if, further, the positive current traverse the spiral in the same direction as the hands of a clock, then the end of the magnet directed towards the person is the negative pole of the magnet. The power of the magnet depends upon the number of spiral windings, and on the thickness of the iron bar. As soon as the current is opened, the magnetism of the iron rod disappears.

Induced or Faradic Current.—If a very long, isolated wire be coiled into the form of a spiral roll, which we may call the **secondary spiral**, and if a similar spiral, the **primary spiral**, be placed near the former, and the ends of the wire of the primary spiral be connected with the poles of a constant battery, every time the current in the primary circuit is made (closed), or broken (opened), a current takes place, or, as it is said, **is induced in the secondary spiral.** If the primary circuit be kept closed, and if the secondary spiral be brought nearer to, or removed further from, the primary spiral, a current is also induced in the secondary spiral (*Faraday*, 1832). The current in the secondary circuit is called the **induced or Faradic current.** When the primary circuit is *closed*, or when the two spirals are brought nearer to each other, the current in the secondary spiral has a direction *opposite* to that in the primary spiral, while the current produced by *opening* the primary circuit, or by removing the spirals further apart, has the *same* direction as the primary. During the time the primary circuit is closed, or when both spirals remain at the same distance from each other, there is no current in the secondary spiral.

Difference between the Opening [break] and Closing [make] Induction Shocks.—[Every time the current is made or broken in the primary circuit a shock is induced in the secondary circuit. The induced shock is called the **make** and the other the **break induction shock.**] The opening and closing shocks induced in the secondary spiral are distinguished from each other in the following respects (fig. 475):—The amount of electricity is the same during the opening, as during the closing shock, but during the **opening shock** the electricity **rapidly** reaches its maximum of intensity and lasts but a short time, while during the **closing shock**, it **gradually** increases, but does not reach the high maximum, and this occurs more slowly. [In fig. 475, P_1 and S_0 are the abscissæ of the primary (inducing) and induced currents respectively. The vertical lines or *ordinates* represent the **intensity** of the current, while the length of the *abscissa* indicates its **duration.** Curve 1 indicates the course of the primary current, and 2, that in the secondary spiral (induced) when the current is *closed*, while at I the primary current is suddenly opened, when it gives rise to the induced current, 4, in the secondary spiral.] The cause of the difference is the following:—When the primary circuit is *made* or *closed*, there is developed in it the **extra-current**, which is *opposite* in direction to the primary current. Hence, it opposes considerable resistance to the complete development of the strength of the primary current, so that the current induced in the secondary spiral must also develop slowly, [thus the **make induction shock** is weakened]. But when the primary spiral is *broken* or *opened*, the extra-current in the latter has the *same* direction as the primary current—there is no extra resistance. [Hence the **break induction shock** is stronger than the make.] The rapid and intense action of the *break* or *opening* induction shock is of great physiological importance.

Break or Opening Shock.—[On applying a **single induction shock** to a nerve or a muscle, the effect is greater with the *break* or *opening* shock, *i.e.*, the **break is stronger** than the make **induction shock.** If the secondary spiral be separated from the primary, so that the induced currents are not sufficient to cause contraction of a muscle when applied to its motor nerve, then, on gradually approximating the secondary to the primary spiral, the *break* or *opening* shock will cause a contraction before the closing one does so.]

Helmholtz's Modification.—Under certain circumstances, it is desirable to **equalise the make and break shocks.** This may be done by greatly weakening the extra-current, which may be accomplished by making the primary spiral of only a few coils of wire. V. Helmholtz accomplishes the same result by introducing a secondary circuit into the primary current. By this arrangement the current in the primary spiral never completely disappears, but at alternate making and breaking this secondary circuit where the resistance is much less it is alternately weakened and strengthened.

[In fig. 476 a wire is introduced between *a* and *f*, while the binding screw *f* is separated from the platinum contact, *c*, of Neef's hammer, but at the same time the screw, *d*, is raised so that it nearly touches Neef's hammer, so that, when the hammer is attached, *c* touches *d*. The current passes from the battery, K, through the pillar, *a*, to *f* in the direction of the arrow, through the primary spiral, P, to the coil of soft wire, *g*, and back to the battery, through *h* and *e*. But *g* is magnetised thereby, and when it is so, it attracts *c* and makes it touch the screw *d*. Thus a secondary circuit, or **short circuit**, is formed through *a*, *b*, *c*, *d*, *e*, which weakens the current passing through the electro-magnet, *g*, so that the elastic metallic spring flies up again and the current through the primary spiral is long-circuited, and thus the process

is repeated. [The break shock in the secondary coil is due to the weakening of the current in the primary coil when the latter is short-circuited. Consequently an extra-current, having a direction reverse to that in the primary current, is induced in the primary coil ; when the shock is made, the break shock is reduced in strength and becomes nearly equal to the make shock. In fig. 475 the lines 1 and 7 indicate the course of the current in the primary circuit at closing (a), and opening (e). It must be remembered that in this arrangement there is always a current passing through the primary spiral P (fig. 476). The dotted lines 6 and 8, above and below S_0, represent the course of the opening (a) and closing shocks (e) in the secondary spiral. Even with this arrangement the opening is still slightly stronger than the closing shock.] The two shocks, however, may be completely equalised by placing a resistance coil or rheostat in the short circuit, which increases the resistance, and thus increases the current through the primary spiral when the short circuit is closed.

[**Extra-current with Helmholtz's arrangement.**—An extra-current is induced in the primary coil both at make and break of the primary circuit. This extra-current may be led off and used for stimulating by connecting electrodes with d and f.]

Unipolar-Induction.—When there is a very rapid current in the primary spiral, not only is

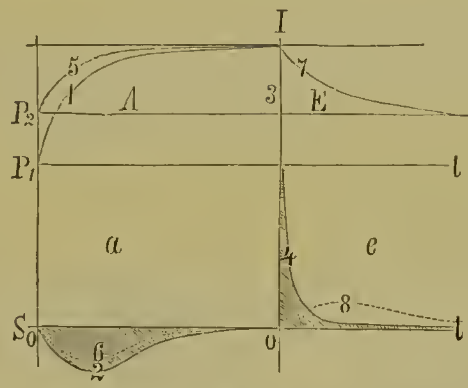


Fig. 475.

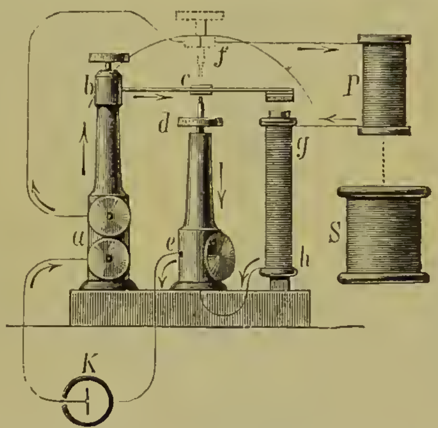


Fig. 476.

Fig. 475.—Scheme of the induced currents. P_1, abscissa of the primary and S_0, of the secondary current ; A, beginning, and E, end of the inducing current ; 1, curve of the primary current weakened by an extra-current ; 3, where the primary current is opened ; 2 and 4, corresponding currents induced in the secondary spiral ; P_2, height, *i.e.*, the strength of the constant inducing current ; 5 and 7, the curve of the inducing current when it is opened and closed during Helmholtz's modification ; 6 and 8, the corresponding currents induced in the secondary circuit. Fig. 476.—Helmholtz's modification of Neef's hammer. As long as c is not in contact with d, $g\ h$ remains magnetic ; thus c is attracted to d and a secondary circuit, a, b, c, d, e is formed ; c then springs back again, and thus the process goes on. A new wire is introduced to connect a with f. K, battery.

there a current induced in the secondary spiral, when its free ends are closed, *e.g.*, by being connected with an animal tissue, but there is also a current when *one* wire is attached to a binding screw connected with one end of the wire of the secondary spiral (p. 663). A muscle of a frog's leg, when connected with this wire, contracts, and this is called a **unipolar induced contraction.** It usually occurs when the primary circuit is opened. The occurrence of these contractions is favoured when the other end of the spiral is placed in connection with the ground, and when the frog's muscle preparation is not completely insulated.

Magneto-Induction.—If a magnet be brought near to, or thrust into the interior of, a coil of wire, it excites a current, and also when a piece of soft iron is suddenly rendered magnetic or suddenly demagnetised. The direction of the current so induced in the spiral is exactly the same as that with Faradic electricity, *i.e.*, the occurrence of the magnetism, on approximating the spiral to a magnet, excites an induced current in a direction opposite to that supposed to circulate in the magnet. Conversely, the demagnetisation, or the removal of the spiral from the magnet, causes a current in the same direction.

Acoustic Tetanus.—If a magnet be rapidly moved to and fro near a spiral, which can easily be done by fixing a vibrating magnetic rod at one end and allowing the other end to swing freely near the spiral, then the pitch of the note of the vibrating rod gives us the rapidity of the induction shocks. If a frog's nerve-muscle preparation be stimulated, we get what Grossmann called "acoustic tetanus."

330. DU BOIS-REYMOND'S INDUCTORIUM—MAGNETO-INDUCTION APPARATUS.—The inductorium of du Bois-Reymond, which is used for physiological purposes, is a modification

of the magneto-electromotor apparatus of Wagner and Neef. A scheme of the apparatus is given in fig. 477. D represents the galvanic battery. The wire from the positive pole, *a*, passes to a metallic column, S, which has a horizontal **vibrating spring**, F, attached to its upper end. To the outer end of the spring a square piece of iron, *e*, is attached. The middle point of the upper surface of the spring [covered with a little piece of platinum] is in contact with a movable screw, *b*. A moderately thick copper wire, *c*, passes from the screw, *b*, to the **primary spiral** or **coil**, *x*, *x*, which contains in its interior a number of pieces of soft iron wire, *i*, *i*, covered with an insulating varnish. The copper wire which surrounds the primary spiral is covered with silk. The wire, *d*, is continued from the primary spiral to a *horse-shoe* piece of soft iron, H, around which it is coiled spirally, and from thence it proceeds, at *f*, back to the negative pole of the battery, *g*. When the current in this circuit—called the **primary circuit**—is closed, the following effects are produced :—The **horse-shoe**, H, becomes magnetic, in consequence of which it attracts the movable spring or Neef's hammer, *e*, whereby the contact of the spring, F, with the screw, *b*, is broken. Thus the current is broken, the horse-shoe is demagnetised, the spring, *e*, is liberated, and being elastic, it springs upwards again to its original position in contact with *b*, and thus the current is re-established. The new contact causes H to be remagnetised, so that it must alternately rapidly attract and liberate the spring, *e*, whereby the primary current is rapidly made and broken between F and *b*.

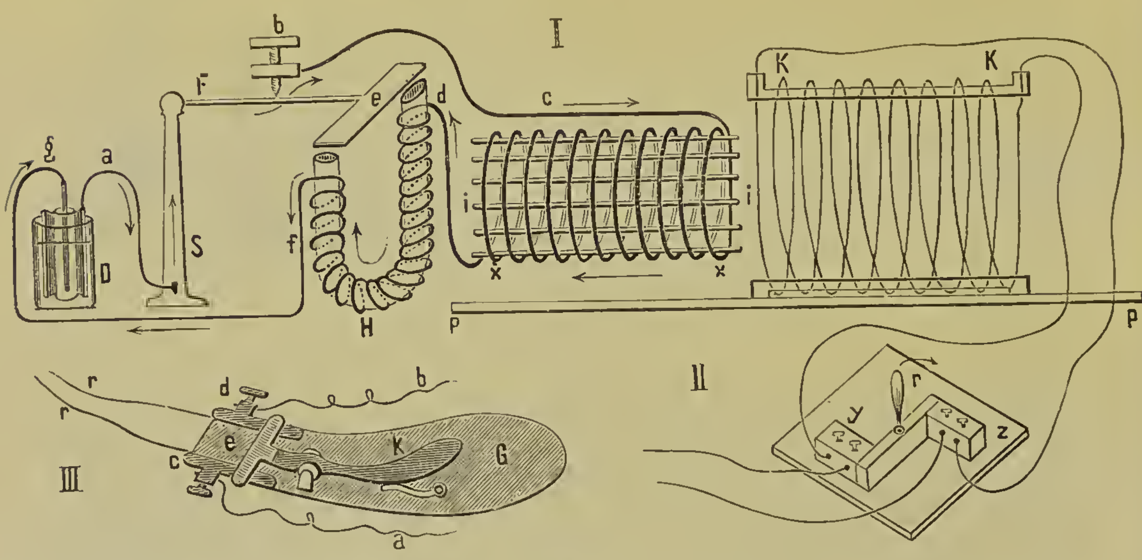


Fig. 477.

I, Scheme of du Bois-Reymond's sledge induction machine. D, galvanic battery ; *a*, wire from + pole, (*g*) – pole ; S, brass upright ; F, elastic spring ; *b*, binding screw ; *c*, wire round primary spiral (*x*, *x*), containing (*i*, *i*,) soft iron wire ; K, K, secondary spiral, with board (*p*, *p*) on which it can be moved ; H, soft iron magnetised by current (*d*, *f*) passing round it. II, key for secondary circuit, as shown it is short-circuited. III, electrodes (*r*, *r*), with a key (K) for breaking the circuit.

A **secondary spiral** or coil (K, K) is placed in the same direction as the primary (*x*, *x*), but having no connection with it. It moves in grooves upon a long piece of wood (*p*, *p*). The secondary spiral consists of a hollow cylinder of wood covered with numerous coils of *thin* silk-covered wire. The secondary spiral, moving in slots, can be approximated to or even pushed entirely over the primary spiral, or can be removed from it to any distance desired.

[Fig. 478 shows the actual arrangement of du **Bois-Reymond's inductorium**. The primary coil (R') consists of about 150 or even 400 coils of **thick** insulated copper wire, the wire being thick to offer slight resistance to the galvanic current, the resistance being equal to about 1·5 ohm. The **secondary** coil (R''') consists of 6000 or 12000 turns of **thin** insulated copper wire arranged on a wooden bobbin. The resistance is equal to about 1350 ohms. The whole spiral can be moved along the board (B) to which a millimetre scale (l) is attached, so that the distance of the secondary from the primary spiral may be ascertained. At the left end of the apparatus is **Wagner's hammer**, as adapted by Neef, which is an automatic arrangement for opening and breaking the primary circuit. When **Neef's hammer is used**, the wires from the battery are connected as in the figure ; but when **single shocks** are required, the wires from the battery are connected with a key, and this again with the two terminals of the primary spiral, S ''and S'''. In the improved form of this apparatus (fig. 479) the secondary spiral is equipoised over a pulley

with a back weight, so that it can move easily in a vertical direction to and from the primary spiral. A. de Watteville has used a form similar to this for a long time.]

According to the law of induction (§ 329), when the primary circuit is closed, a current is induced in the secondary circuit in a direction the *reverse* of that in the primary, while, when it is opened, the induced current has the *same* direction. Further, according to the laws of magneto-induction, the magnetisation of the iron rods (i, i) within the primary spiral (x, x), causes a *reverse* current in the secondary spiral (K, K), while the demagnetisation of the iron rods, on opening the primary circuit, causes an induced current in the *same* direction. Thus, we explain the much more powerful action of the opening or break shock as compared with the closing or make shock (p. 678). [The direction of the *inducing* current remains the *same*, while the direction of the induced currents are constantly reversed.]

The **magneto-induction** (R) apparatus of Pixii, as improved by Stöhrer, consists of a very powerful horse-shoe **steel magnet** (fig. 480). Opposite its two poles (N and S) is a horse-shoe-shaped piece of iron (H), which rotates on a horizontal axis (a,b). On the ends of the horse-shoe are fixed wooden bobbins (c, d), with an insulated wire coiled round them. When the horse-shoe is at rest, as in the figure, it becomes magnetised by the steel magnet, while in the wires of both bobbins (c and d) an electric current is developed every time the horse-shoe is demagnetised and again magnetised. When the bobbins rotate in front of the magnet as each coil approaches one pole, a current is induced, and similarly when it is carried past the pole of the magnet, so that four currents are induced in each coil by a single rotation. By means of Stöhrer's commutator (m, n) attached to the spindle (a, b), and the

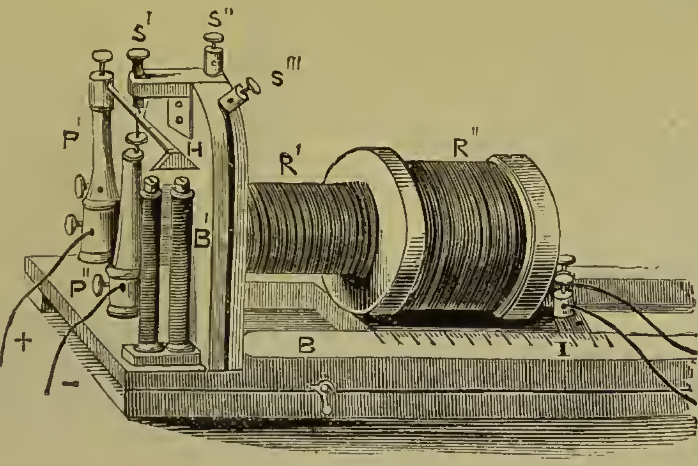


Fig. 478.

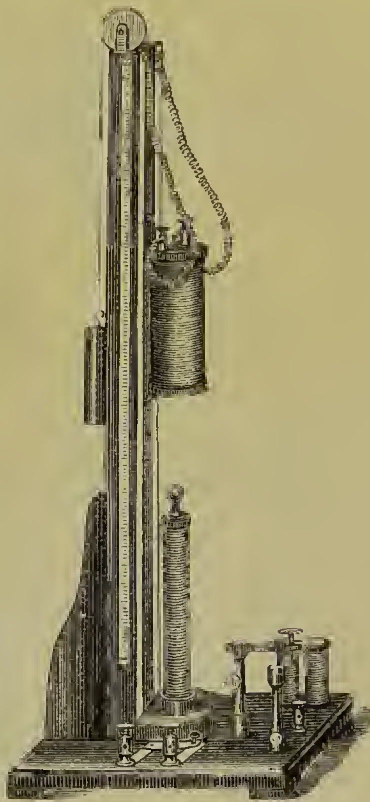


Fig. 479.

Fig. 478.—Induction apparatus of du Bois-Reymond. R′, primary, R″, secondary spiral; B, board on which R″ moves; 1, scale; + –, wires from battery; P′, P″, pillars; H, Neef's hammer; B′, electro-magnet; S′, binding screw touching the steel spring (H); S″ and S‴, binding screws to which to attach wires where Neef's hammer is not required. Fig. 479.—New form of du Bois-Reymond's inductorium.

divided metal plates (y, z) which pass to the electrodes, the two currents induced in the bobbins are obtained in the same direction.

Keys, or arrangements for opening or closing a circuit, are of great use. Fig. 477, II, shows a scheme of the **friction key** of du Bois-Reymond, introduced into the secondary circuit. It consists of two brass bars (z and y) fixed to a plate of ebonite, and as long as the key is down on the metal bridge (y, r, z) it is "**short-circuited**," *i.e.*, the conduction is so good through the thick brass bars that none of the current goes through the wires leading from the left of the key. When the bridge (r) is lifted the current is opened. [Fig. 481 shows the form of the key, v being a screw wherewith to clamp it to the table.] Similarly the key electrodes (III) may be used, the current being made as soon as the spring connecting-plate (c) is raised by pressing upon k. This instrument is opened by the hand; a, b are the wires from the battery or induction machine; r, r, those going to the tissue; G, the handle of the instrument.

[**Plug Key.**—Other forms of keys are in use, *e.g.*, fig. 482, the plug key, the two brass plates to which the wires are attached being fixed on a plate of ebonite. The brass plug is used to connect the two brass plates. All these are dry **contacts**, but sometimes a **fluid contact** is used,

as in the mercury key, which merely consists of a block of wood with a cup of mercury in its centre. The ends of the wires from the battery dip into the mercury ; when both wires dip into the mercury the circuit is made, and when one is out it is broken.]

[**Capillary Contact Key.**—Where an ordinary mercury key is used to open and close the primary circuit, the layer of oxide formed on the surface by the opening spark disturbs the con-

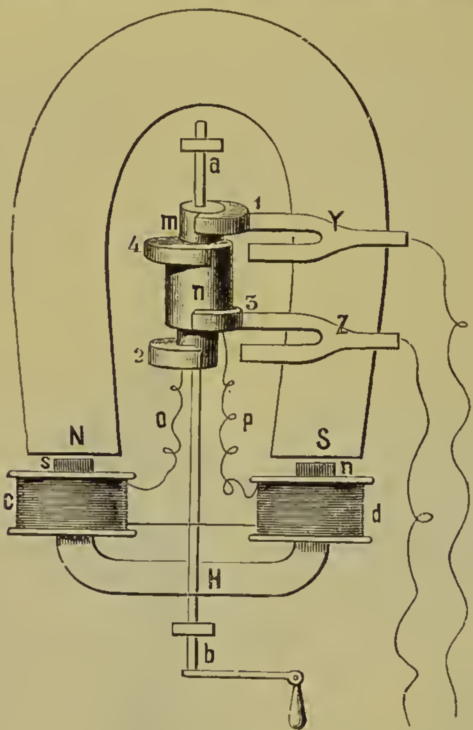


Fig. 480.
Magneto-induction apparatus, with Stöhrer's commutator.

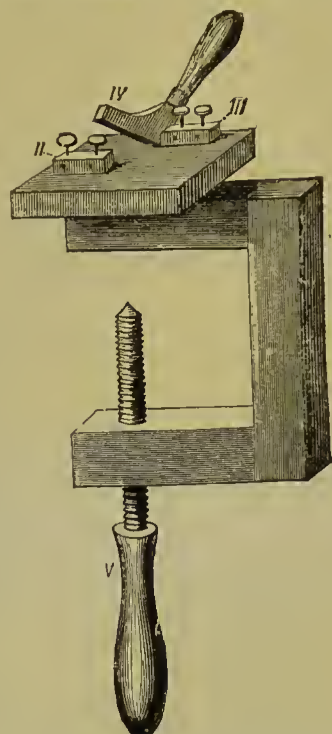


Fig. 481.
Du Bois-Reymond's friction key.

duction after a short time ; hence, it is advisable to wash the surface of the mercury with a dilute solution of alcohol and water. A handy form of "capillary contact" is shown in fig. 483, such as was used by Kronecker and Stirling in their experiments on the heart. A glass T-tube is provided at the crossing point with a small opening (*a*). The vertical tube (*b*) is bent in the form of a U, and filled so full with mercury that the convex surface of the latter projects

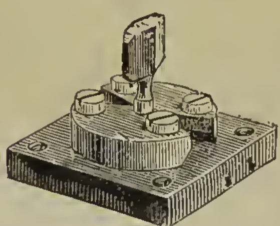


Fig. 482.

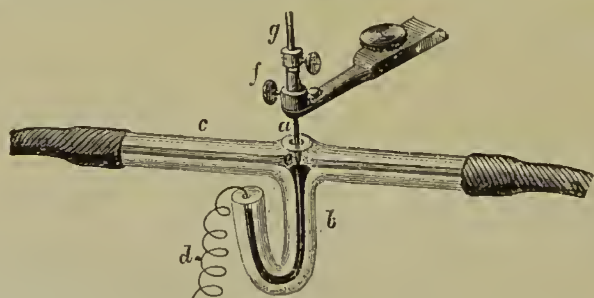


Fig. 483.

Fig. 482.—Plug key. Fig. 483.—Capillary contact. *c*, vibrating platinum style adjustable by *f* and *g* and dipping into mercury at *a* ; *b*, bent tube filled with mercury, into which dips a wire (*d*) ; *a*, opening in cross tube (*c*).

within the lumen of the transverse tube (*c*). One end of *c* is connected with a Mariotte's flask containing diluted alcohol, and the supply of the latter can be regulated by means of a stop-cock. The fluid flows over the apex of the mercury and keeps it clean. The vibrating platinum style (*c*) is attached to the end of a rod, which in turn is connected with the positive pole of the battery, while the platinum wire (*d*) is connected with the negative pole of the "battery."]

331. ELECTRICAL CURRENTS IN RESTING MUSCLE AND NERVE—SKIN CURRENTS.—Methods.—In order to investigate the laws of the muscle-current, we must use a muscle composed of parallel fibres, and with a simple arrangement of its fibres in the form of a prism or cylinder (fig. 484, I and II). The **sartorius muscle of the frog** supplies these conditions. In such a muscle, we distinguish the **surface** or the **natural longitudinal section**; its **tendinous ends** or the **natural transverse section**; further, when the latter is divided transversely to the long axis, the **artificial transverse section** (fig. 484, I, *c*, *d*); lastly, the term **equator** (*a*, *b*–*m*, *n*) is applied to a line so drawn as exactly to divide the length of the muscle into halves. As the currents are very feeble, it is necessary to use a **galvanometer** with a periodic damped magnet (figs. 459, I, and 471), or a tangent mirror-boussole similar to that used for thermo-electric purposes (fig. 230). The wires leading from the tissue are connected with non-polarisable electrodes (fig. 459, P,P).

The **capillary-electrometer** of Lippmann may be used for detecting the electrical current of a muscle or nerve (fig. 485). A thread of mercury enclosed in a capillary tube and touching a conducting fluid, *e.g.*, dilute sulphuric acid, is displaced by the constant current, in consequence of the polarisation taking place at the point of contact altering the constancy of the capillarity of the mercury. The displacement of the mercury which the observer (B) detects by the aid of the microscope (M) is in the direction of the positive current. R is a capillary glass tube, filled from above with mercury, and from below with dilute sulphuric acid. Its lower narrow end opens into a wide glass tube, provided below with a platinum wire fused into it and filled with Hg (*q*), and this again is covered with dilute sulphuric acid (*s*). The wires are connected with non-polarisable electrodes applied to the + and − surfaces of the muscle. On closing the circuit, the thread of mercury passes downwards from *c* in the direction of the arrow.

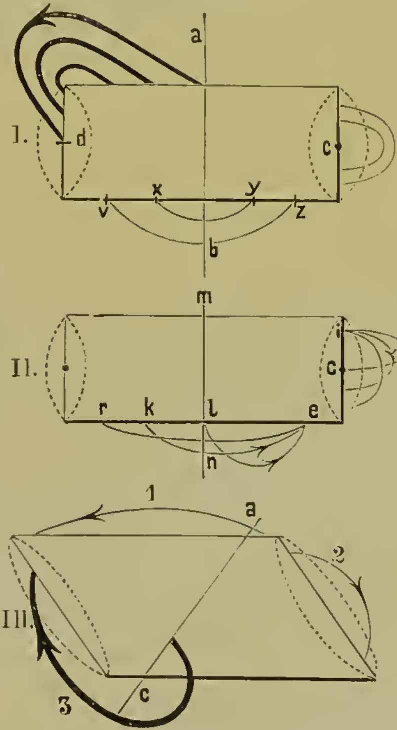


Fig. 484.
Scheme of the muscle-current.

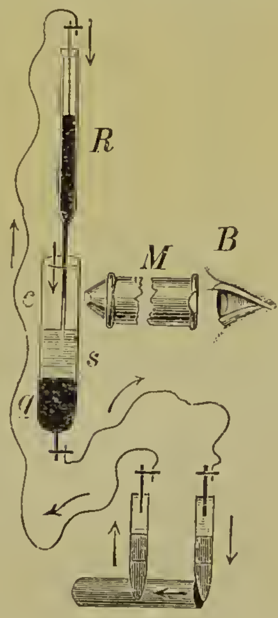


Fig. 485.
Capillary electrometer. R, mercury in tube; capillary tube; *s*, sulphuric acid; *q*, Hg; B, observer; M, microscope.

Compensation of a current.—The strength of the current in animal tissues is best measured by the compensation method of Poggendorf and du Bois-Reymond. A current of known strength, or which can be accurately graduated, is passed in an opposite direction through the same galvanometer or boussole, until the current from the animal tissue is just neutralised or compensated. [When this occurs, the needle deflected by the tissue-current returns to zero. The principle is exactly the same as that of weighing a body in terms of some standard weights placed in the opposite scale-pan of the balance.]

[Hermann calls the current obtained from an **injured muscle**, *i.e.*, one on which an artificial transverse or other section has been made, a **demarcation-current**, while the currents obtained when such a muscle contracts he calls **action-currents**. This section deals with demarcation-currents, or the muscle-current of du Bois-Reymond.]

1. Perfectly fresh **uninjured muscles** yield **no current**, and the same is true of dead muscle (*L. Hermann*, 1867).

2. **Strong electrical** currents are obtained when the *artificial transverse section* of a muscle is placed on one of the cushions of the non-polarisable electrodes (fig. 459 I, M), while the *longitudinal surface* is in connection with the other (*Nobili, Matteucci, du Bois-Reymond*). The **direction of the current** is from the (positive) longitudinal section to the (negative) transverse section in the conducting wires (*i.e.*, within the muscle itself from the transverse to the longitudinal section (figs. 459, I, and 484, I)). This current is stronger the nearer one electrode is to the equator and the other to the centre of the transverse section; while the strength diminishes the nearer the one electrode is to the end of the surface, and the other to the margin of the transverse section.

Smooth muscles also yield similar currents between their transverse and longitudinal surfaces (§ 334, II.).

3. **Weak electrical currents** are obtained when—(*a*) two points at unequal distances from the equator are connected with the galvanometer, the current then passes from the point near the equator (+) to the point lying further from it (−), but of course this direction is reversed within the muscle itself (fig. 484, II, *ke* and *le*). (*b*) Similarly weak currents are obtained by connecting points of the transverse section at unequal distances from the centre, in which case the current outside the muscle passes from the point lying nearer the edge of the muscle to that nearer the centre of the transverse section (fig. 484, II, *i*, *c*).

4. When two points on the surface are **equidistant** from the equator (fig. 484, I, *x*, *y*, *v*, *z*,—II, *r*, *e*), or two equidistant from the centre of the transverse section (II, *c*) are connected, no current is obtained, because the points are iso-electrical, that is of equal potential.

5. If the artificial transverse section of the muscle be **oblique** (fig. 484, III), so that the muscle forms a **rhomb**, the conditions obtaining under III are disturbed. The point lying nearer to the *obtuse* angle of the transverse section or surface is positive to the one lying near to the acute angle. The equator is oblique (*a*, *c*). These currents are called "*deviation currents* or *inclination currents*" by du Bois-Reymond, and their course is indicated by the lines 1, 2, and 3.

The **electro-motive force of a strong muscle-current** (frog) is equal to 0·05 to 0·08 of a Daniell's element; while the strongest deviation current may be 0·1 Daniell. The muscles of a curarised animal at first yield stronger currents; *fatigue* of the muscle diminishes the strength of the current (*Roeber*), while it is completely **abolished when the muscle dies**. *Heating* a muscle increases the current; but above 40° C. it is diminished (*Steiner*). *Cooling* diminishes the electro-motive force. The warmed *living* muscular and nervous substance is positive to the cooler portions (*Hermann*); while, if the *dead* tissues be heated, they behave practically as indifferent bodies as regards the tissues that are not heated.

6. The **passive nerve** behaves like muscle, as far as 1, 2, and 3 are concerned. [If one electrode be placed on the longitudinal surface and another on the artificial transverse section of a nerve, and the current led off to a galvanometer, the needle of the latter is slightly deflected by the "**nerve-current**," the direction of the current being from the + longitudinal surface through the galvanometer to the − transverse section.]

The **electro-motive force of the strongest nerve-current**, according to du Bois-Reymond, is 0·02 of a Daniell. Heating a nerve from 15° to 25° C. increases the nerve-current, while high temperatures diminish it (*Steiner*).

7. If the two transversely divided ends of an excised **nerve**, or two points on the surface equidistant from the equator, be tested, a current—the **axial current**—flows in the nerve-fibre in the opposite direction to the direction of the normal impulse in the nerve; so that in centrifugal nerves it flows in a centripetal direction and in centripetal nerves in a centrifugal direction (*Mendelssohn and Christiani*).

The electro-motive force increases with the length of the nerve and with the area of its transverse section. Fatigue (*e.g.*, tetanic stimulation) weakens it, especially in motor nerves, and to a less extent in centripetal nerves.

Rheoscopic Limb.—The existence of a **muscle-current** may be proved **without the aid of a galvanometer**:—1. By means of a sensitive nerve-muscle preparation of a frog, or the so-called "**physiological rheoscope**" or "**rheoscopic limb.**" Place a moist conductor on the transverse and another on the longitudinal surface of the gastrocnemius of a frog. On placing the sciatic nerve of a nerve-muscle preparation of a frog on these conductors, so as to bridge over or connect their two surfaces, contraction of the muscle connected with the nerve occurs at once; and the same occurs when the nerve is removed.

[**Nerve-muscle Preparation.**—This term has been used on several occasions. It is simply the sciatic nerve with the gastrocnemius of the frog attached to it (fig. 486). The sciatic nerve is dissected out entire from the vertebral column to the knee; the muscles of the thigh separated from the femur, and the latter divided about its middle, so that the preparation can be fixed in a clamp by the remaining portion of the femur; while the tendon of the gastrocnemius is divided near to the foot. If a straw flag is to be attached to the foot, do not divide the tendo Achillis.]

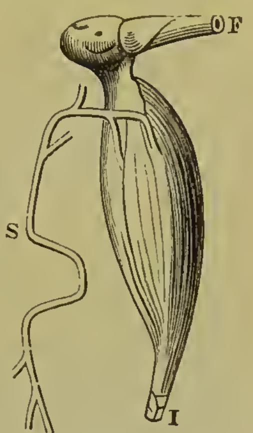


Fig. 486.
Nerve-muscle preparation of a frog. F, femur; S, sciatic nerve; I, tendo Achillis.

Make a transverse section of the gastrocnemius muscle of a frog's nerve-muscle preparation, and allow the sciatic nerve to fall upon this transverse section; the limb will contract as the muscle-current from the longitudinal to the transverse surface now traverses the nerve (*Galvani*, *Al. v. Humboldt*). These experiments have long been known as "**contraction without metals.**"

[Use a nerve-muscle preparation, or, as it is called, a physiological limb. Hold the preparation by the femur, and allow its own nerve to fall upon the gastrocnemius, and the muscle will contract, but it is better to allow the nerve to fall suddenly upon the cross-section of the muscle. The nerve then completes the circuit between the longitudinal and transverse section of the muscle, so that it is stimulated by the current from the latter, the nerve is stimulated, and through it the muscle. That it is so is proved by tying a thread round the nerve near the muscle, when the latter no longer contracts.]

2. **Self-Stimulation of the Muscle.**—We may use the **muscle-current** of an isolated muscle to stimulate the latter directly and cause it to contract. If the transverse and longitudinal surfaces of a curarised frog's nerve-muscle preparation be placed on non-polarisable electrodes, and the circuit be closed by dipping the wires coming from the electrodes in mercury, then the muscle contracts. Similarly a **nerve** may be stimulated with its own **demarcation-current** (*du Bois-Reymond and others*). If the lower end of a muscle with its transverse section be dipped into normal saline solution (0·6 per cent. NaCl), which is quite an indifferent fluid, this fluid forms an accessory circuit between the transverse and adjoining longitudinal surface of the muscle, so that the muscle contracts. Other indifferent fluids used in the same way produce a similar result.

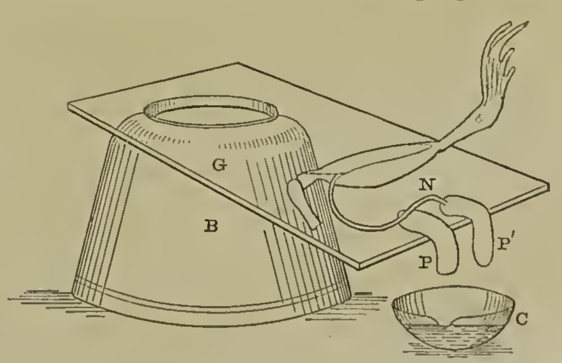


Fig. 487.
Kühne's nerve demarcation-current experiment.

[**Kühne's Experiment** (fig. 487).—The demarcation-current of the nerve of a nerve-muscle preparation may be used as the stimulus to that nerve on completing the circuit. On an earthenware bowl (B) is fixed a glass plate (G) and thin rolls

of modeller's clay (P P′) are bent over G. A nerve-muscle preparation is placed with its nerve (N) on the clay, touching the latter with its transverse and longitudinal surfaces. On dipping the clay into a vessel containing normal saline (C), the muscle contracts, and on withdrawing the normal saline, it again contracts. In this case the nerve is stimulated by the completion of the circuit of its own demarcation-current.]

3. **Electrolysis.**—If the muscle-current be conducted through *starch mixed with potassic iodide*, then the iodine is deposited at the + pole, where it makes the starch blue.

Frog Current.—It is asserted that the total current in the body is the sum of the electrical currents of the several muscles and nerves which, in a frog deprived of its skin, pass from the tip of the toes toward the trunk, and in the trunk from the anus to the head. This is the "*corrente propria della rana*" of Leopoldo Nobili (1827), or the "frog-current" of du Bois-Reymond. In mammals, the corresponding current passes in the opposite direction.

When the nerves have lost their excitability in the condition of narcosis after the administration of ether or chloroform, the muscle-current may even be slightly increased (*Biedermann*).

After death, the currents disappear sooner than the excitability (*Valentin*); they remain longer in the muscle than the nerves, and in the latter they disappear sooner in the central portions. If the nerve-current after a time become feeble, it may be strengthened by making a new transverse section of the nerve. A motor nerve completely paralysed by **curare** gives a current (*Funke*), and so does a nerve beginning to undergo degeneration, even two weeks after it has lost its excitability. Muscles in a state of **rigor mortis** give currents in the opposite direction, owing to inequalities, which take place during decomposition. The nerve-current is reversed by the action of boiling water or drying.

Currents from Skin and Mucous Membranes.—In the **skin** of the frog the outer surface is +, the inner is − (*du Bois-Reymond*), and the same is true of the **mucous membrane** of the intestinal tract (*Rosenthal*), the cornea (*Grünhagen*), as well as the **non-glandular skin** of fishes (*Hermann*) and molluscs (*Oehler*). Currents are also manifested by **glands** (§ 145).

332. CURRENTS OF STIMULATED MUSCLE AND NERVE—ACTION-CURRENTS.—1. Negative Variation of the Muscle-Current.—If a muscle, which yields a strong electrical current, be thrown into a state of tetanic contraction by stimulating its motor nerve, then, when the muscle contracts, there is a **diminution of the muscle-current**, and occasionally the needle of the galvanometer may swing almost to zero. This is the "**negative variation of the muscle-current**" (*du Bois-Reymond*). It is larger the greater the primary deflection of the galvanometer needle and the more energetic the contraction.

After tetanus the muscle-current is weaker than it was before. If the muscle was so placed upon the electrodes that the current was "feeble," equally during tetanus there is a diminution of this current. In the inactive arrangement, the contraction of the muscle has no effect on the needle. If the muscle be prevented from shortening, as by keeping it tense, the negative variation still takes place.

2. **Current during Tetanus.**—An *excised* frog's muscle *tetanised* through its *nerve* shows electro-motive force—the so-called "**action-current.**" In a tetanised frog's gastrocnemius, there is a *descending* current. In completely uninjured human muscles, however, thrown into tetanus by acting on their nerves, there is no such current (*L. Hermann*); similarly, in *quite uninjured* frog's muscles, as well as when these muscles are *directly* and *completely tetanised*, there is no current.

3. **Muscle-Current accompanying the contraction-wave.**—If one end of a muscle be directly excited with a momentary stimulus, so that the *contraction-wave* (§ 299) rapidly passes along the whole length of the muscular fibres, then each part of the muscle, successively and immediately before it contracts, becomes negatively electrical. It is usually stated that the "**contraction-wave**" is **preceded** by a "**negative wave**" of the muscle-current, and that the latter occurs during the **latent period** (?). Both waves have the same velocity, about 3 metres per second. The negative wave, which first increases and then diminishes, lasts at each point only 0·003

second (*Bernstein*). [Suppose two points, A and B, on the longitudinal surface of a muscle to be led off with non-polarisable electrodes to a galvanometer. There will be no deflection of the needle, as the points are iso-electrical. If a single induction shock be applied at one end of the muscle, a contraction-wave will be propagated along the muscle. It is usually stated that preceding the contraction-wave, however, a **wave of negativity** will pass along the fibre. It will reach A before B, so that A will be negative to B and to the rest of the fibre, and the needle will be deflected. The wave of negativity as it travels will reach B, and make B negative to the rest of the fibre, and to A, from which the negativity is disappearing. This will cause the needle to be deflected in the opposite direction, so that a single wave of contraction in a muscle is preceded by two currents of different phases, *i.e.*, it gives rise to a **diphasic variation** or change. Burdon-Sanderson, however, has shown that the electro-motive changes, instead of preceding the change of muscular form, actually accompanies the latter, so that the view that it occurs during the latent period must be abandoned (p. 594, fig. 395).]

4. **During a single Contraction.**—A **single contraction** also shows a muscle-current. [The electrical variation takes place during the latent period of the muscular contraction, so that it precedes the latter (?). The variation begins 0·1″ to ·04″ after excitation, while the contraction does not begin until ·11″ to ·33″ (*Waller*). A frog's muscle may be made to record its contraction, and simultaneously the variation of the electrical current, as ascertained by the capillary electrometer, may be photographed (fig. 488), and the same may be done in the case of the heart (fig. 489). The capillary electrometer may with advantage be employed to measure this time-difference, the electrical and the mechanical events being simultaneously recorded.]

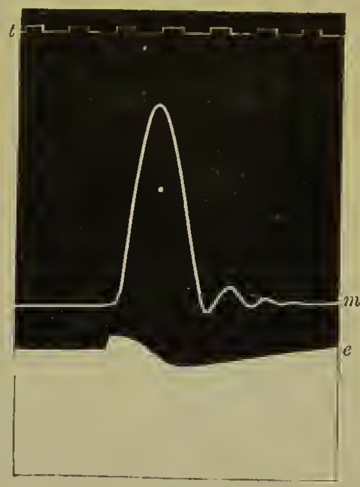


Fig. 488.

Frog. Gastroenemius led off to electrometer from the middle of the muscle and from the tendon. Contraction excited by a single break induction shoek applied to the sciatic nerve. *e*, eleetrometer; *m*, musele; *t*, time in $\frac{1}{20}$th sec. (musele to H_2SO_4; tendon to Hg) (*Waller*).

The **diphasic variation.**—1st phase middle negative to end; 2nd phase and negative to middle begins about ·01″ before the eommencement of musenlar eontraetion (*Waller*).

The variation is diphasie—1st phase base negative to apex; 2nd phase apex negative to base (*Waller*). The first phase begins $\frac{1}{10}$″ before the commeneement of contraetion.

One of the best objects for this purpose is the **contracting heart,** which is placed upon the non-polarisable electrodes connected with a sensitive galvanometer. Each beat of the heart causes a deflection of the needle, which occurs *before* the contraetion of the cardiac muscle (*Kölliker and H. Müller*). The electrical disturbance in the muscle causing the negative variation always precedes the aetual contraction (*v. Helmholtz*, 1845). Still it lasts throughout the whole duration of the contraction (*Lee*). When the completely uninjured frog's gastrocnemius contracts by stimulating the nerve, there is at first a descending and then an ascending current (*Sig. Mayer*, § 334, II.).

More exact observations on the **electrical processes of the pulsating heart** show that complicated phenomena occur. With every beat of the heart, first the apex, and then the base of the ventricle becomes negative (*Fredericq and Waller*), so that necessarily there is a **diphasic variation** with each beat (fig. 489). If the heart be arrested in diastole by stimulation of the vagus (§ 369), there is a *positive* variation of the muscle-current (*Gaskell, Fano*). Waller has demonstrated a true electrical variation of the human intact heart.

[**Heart.**—Gaskell has shown that when the vagus of a tortoise is stimulated so

as to arrest its heart in diastole, the action of the inhibitory nerve is accompanied by a *positive* electrical variation of the heart-current, while stimulation of the sympathetic (augmentor) nerve causes an electrical variation of the same sign as that caused by a contraction in the non-beating tissue of the ventricle of the toad. In both cases the respective nerves can produce their electrical effect after the heart has been brought to standstill by the application of muscarin to the sinus.

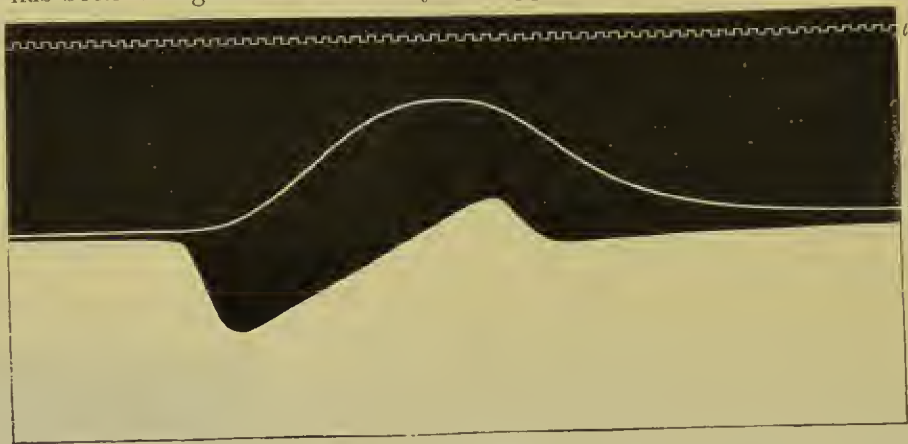


Fig. 489.

Frog's heart. Spontaneous contraction. *e*, *e*, electrometer; *h*, *h*, heart's contraction; *t*, *t*, time in $\frac{1}{20}$th sec. (apex to H_2SO_4, base to Hg) (*Waller*).

These experiments are of the utmost importance in connection with the theory of the action of these nerves on the heart (§ 370), and the mode of action of poisons on the heart itself.]

[Waller has succeeded in showing the electrical variation occurring during the beat of the **human heart** in an uninjured person. The readings are made by photographing the oscillations of the mercury of a capillary electrometer. The currents obtained are due to the ventricles just as much as to the auricles. There is a diphasic variation, beginning with a first phase of short duration, which shows that the apex is negative to the base, and this is followed by a stronger variation in the opposite direction, which shows that during this period the base of the ventricle is negative to the apex. Waller therefore infers that the state of excitement of the ventricle begins at the apex and is propagated to the base. Owing to the oblique position of the human heart, the variation is obtained when the right and left hand, or the right hand with one of the feet, are connected with the electrometer, but not when one of the feet and the left hand are so connected.]

Secondary Contraction.—A nerve-muscle preparation may be used to demonstrate the electrical changes that occur during a **simple contraction**. If the sciatic nerve, A, of such a preparation be placed upon another muscle B, as in fig. 490, then every time the latter, B, contracts, the frog's muscle, A, connected with the nerve also contracts.

If the nerve of a frog's nerve-muscle preparation be placed on a contracting **mammalian heart**, then a contraction of the muscle occurs with every beat of the heart (*Matteucci*, 1842). The diaphragm, even after section of the phrenic nerve, especially the left, also contracts during the heart-beat (*Schiff*). This is the "**secondary contraction**" of Galvani.

[**Secondary Contraction from Muscle to Muscle, and Muscle-press** (*Kühne*).—If 5 mm. of one end of the sartorius of a curarised frog be laid upon a corresponding 5 mm. of the other sartorius, so that both muscles are in line, and if the surfaces of contact be pressed together, either by an ebonite press or other means, on stimulating the free end of one of the muscles—either electrically, mechanically, or chemically—the other muscle also contracts, and if the first one be tetanised, the second one also is thrown into tetanus. The experiment may be repeated with five or six muscles in line. The conduction is interrupted at once by ligature

of the muscle. The second muscle contracts, because it is stimulated directly by the **action-currents** of the contracting muscular fibres. The effect is prevented by introducing, between the overlapping ends of the muscle, a thin plate of gutta-percha, tinfoil, or any insulator. This experiment of Kühne's shows us how important a *rôle* electrical phenomena play in connection with muscular contraction. Secondary contraction from nerve has long been known.]

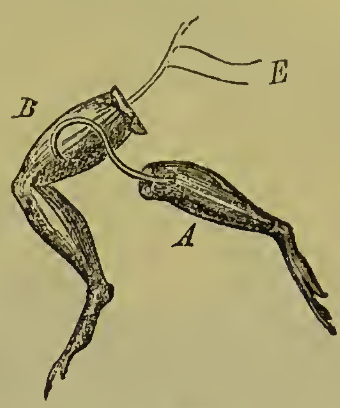


Fig. 490.
Secondary contraction. The sciatic nerve of A lies on B; E, electrodes applied to the sciatic nerve of B.

Secondary Tetanus.—Similarly, if a nerve of a nerve-muscle preparation be placed on a muscle which is tetanised, then the former also contracts, showing "secondary tetanus" (*du Bois-Reymond*). The latter experiment is regarded as a proof that, during the process of negative variation in the muscle, many successive variations of the current must take place, as only rapid variations of this kind can produce tetanus by acting on a nerve—*continuous* variations being unable to do so.

Usually, there is no secondary tetanus in a frog's nerve-muscle preparation when it is laid upon a muscle which is tetanised voluntarily, or by chemical stimuli, or by poisoning with strychnin (*Hering, Kühne*); still, Lovèn has observed secondary strychnin tetanus composed of six to nine shocks per second. Observations with a sensitive galvanometer, or Lippmann's capillary electrometer (fig. 485), show that the spasms of strychnin poisoning, as well as a voluntary contraction, are discontinuous processes (*Lovèn*, p. 601).

Biedermann observed that striped muscle, under the influence of the vapour of **ether**, passes into a condition in which it shows no obvious change of form or movement when it is stimulated, whilst at the spot stimulated there are galvanometric variations of the same strength as occurred during stimulation before the action of the ether. Owing to the abolition of the power of conductivity, they can only manifest themselves locally.

5. **Negative Variation in Nerve.**—If a **nerve** be placed with its artificial transverse section on one non-polarisable electrode, and its longitudinal surface on the other, and if it be stimulated electrically, chemically, or mechanically, the nerve-current is also diminished (*du Bois-Reymond*). This **negative variation** is propagated towards *both* ends of a nerve, and is composed of very rapid, successive, periodic interruptions of the original current, just as in a contracted muscle (*Bernstein*). Hering succeeded in obtaining from a nerve, as from a muscle, a secondary contraction or secondary tetanus. The amount of the negative variation depends upon the extent of the primary deflection, also upon the degree of nervous excitability, and on the strength of the stimulus employed. The negative variation occurs on stimulating with **tetanic** as well as with **single shocks.** The negative variation is not observed in completely uninjured nerves.

Hering found that the negative variation of the nerve-current caused by tetanic stimulation is followed by a *positive* variation, which occurs immediately after the former, *i.e.*, it is diphasic. It increases to a certain degree with the duration of the stimulation, as well as with the strength of the stimulus, and with the drying of the nerve (*Head*). (*Effect of Electrotonus*, § 335, I.).

Negative Variation in the Spinal Cord.—This is the same as in nerves generally. If a current be conducted from the transverse and longitudinal surfaces of the upper part of the medulla oblongata, we observe *spontaneous*, intermittent, *negative variations*, perhaps due to the intermittent excitement of the nerve-centres, more especially of the respiratory centre. Similar variations are obtained reflexly by single stimuli applied to the sciatic nerve, while strong stimulation by common salt or induction shocks inhibits them. [Gotch and Horsley obtained "action currents" from the cord when the motor areas of the brain were stimulated (§ 375).]

Velocity of the Negative Variation.—The process of negative variation is propagated at a measurable velocity along the nerve, most rapidly at 15° to 25° C. (*Steiner*), and at the same rate as the velocity of the nervous impulse itself, about 27 to 28 metres per second. The duration of a single variation (of which the process of negative variation is composed) is only 0·0005 to 0·0008 second, while the **wave-length** in the nerve is calculated by Bernstein at 18 mm.

Differential Rheotome.—J. Bernstein estimated the **velocity of the negative variation** in a nerve by means of a differential rheotome thus (figs. 491, 492):—A long stretch of a nerve (N n) is so arranged that at *one* end of it (N) its transverse and longitudinal surfaces are connected with a galvanometer (G), [*i.e.*, an artificial transverse section and the longitudinal surface are

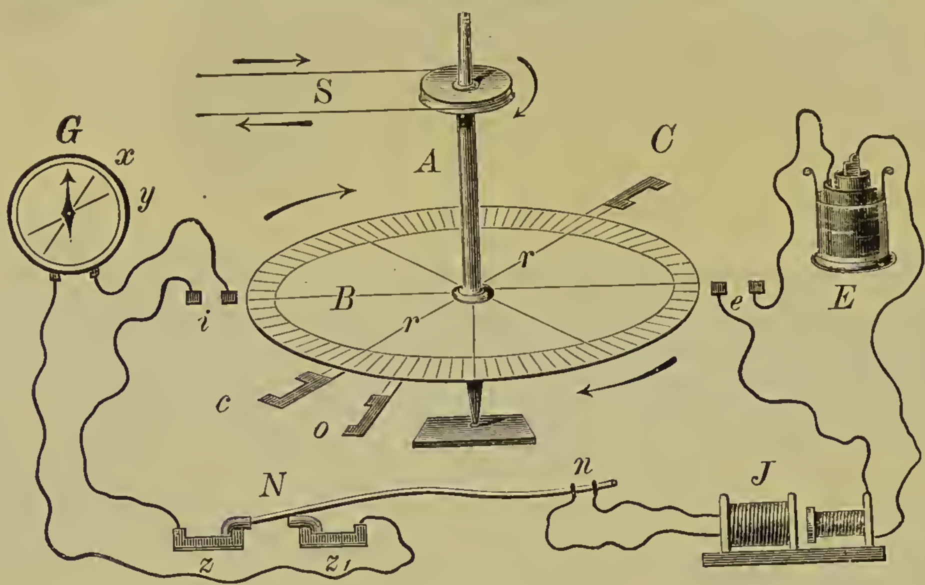


Fig. 491

Scheme of Bernstein's differential rheotome; N n, nerve; J, induction machine; G, galvanometer; x, y, deflection of needle; E, battery and primary circuit with C for opening it at o; c, for closing galvanometer circuit; z z, electrodes in galvanometer circuit; S, motor.

led off by non-polarisable electrodes to the galvanometer], while at the *other* end (n) are placed the electrodes of an induction machine (J) [*i.e.*, the stimulating electrodes]. A disc (B) rapidly rotating on its vertical axis (A) has an arrangement (C) at one point of its circumference, by means of which the current of the primary circuit (E) is rapidly opened and closed during each revolution. This causes, with each rotation of the disc, an opening and a closing shock to be applied to the end of the nerve through the stimulating electrodes (n). At the diametrically opposite part of the circumference is an arrangement (c) by which the galvanometer circuit is closed and opened during each revolution. Thus the **stimulation** of the nerve and the closing of the galvanometer circuit occur at the same moment. On rapidly rotating the disc, the galvanometer indicates a strong nerve-current, an excursion of the magnetic needle to y. At the moment of stimulation, the negative variation has not yet reached the other end of the nerve. If, however, the arrangement which closes the galvanometer circuit be so displaced along the circumference (to o) so that the galvanometer circuit is closed somewhat *later* than the nerve is stimulated, then the current is **weakened** by the negative variation (the needle passing backward to x). When we know the velocity of rotation of the disc, it is found that the time for the distance of the displaced closing arrangement for the galvanometer circuit must be equal to the velocity at which the impulse causing the negative variation passes along a given distance of nerve from N to n.

The negative variation is absent in **degenerated nerves** as soon as they lose their excitability.

Retinal and Eye Currents.—If a freshly-excised eyeball be placed on the non-polarisable electrodes connected with a galvanometer, and if light fall upon the eye, then the normal **eye-current** from the cornea (+) to the transverse section of the optic nerve (−) is at first increased.

Yellow light is most powerful, and less so the other colours (*Holmgren, M'Kendrick and Dewar*). The inner surface of the *passive* retina is positive to the posterior. When the retina is illuminated there is a double variation, a negative variation with a preliminary positive increase; while, when the light ceases, there is a simple positive variation. Retinæ, in which the visual purple has disappeared owing to the action of light, show smaller variations (*Kühne and Steiner*).

Stimulation of the secretory nerves of glandular membranes, besides causing secretion, affects the current of rest (*Roeber*). This **secretion-current** passes in

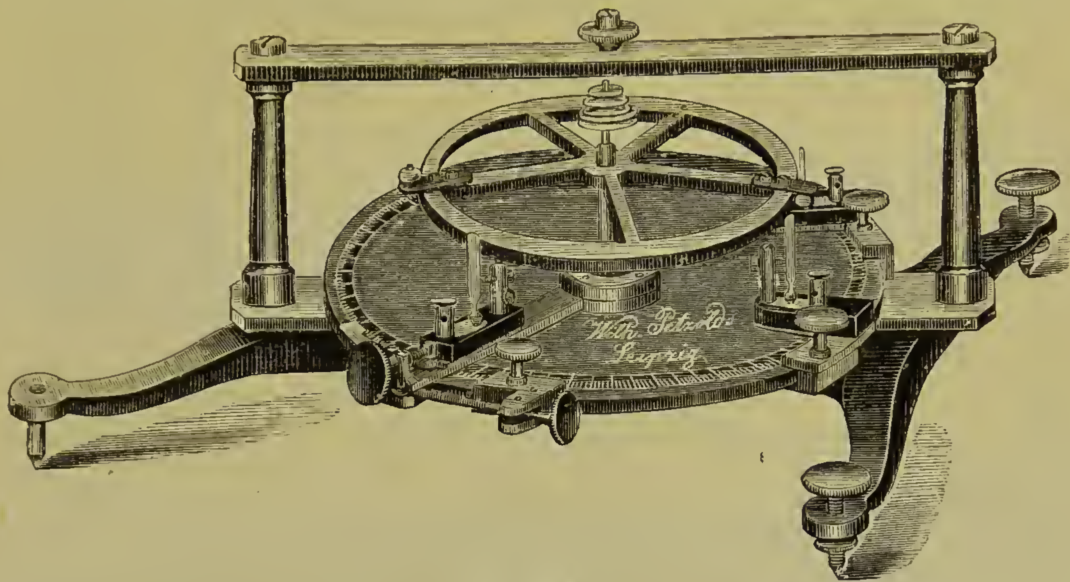


Fig. 492.
General view of a differential rheotome, as made by Petzold of Leipzig.

the *same* direction in the skin of the frog and warm-blooded animals as the current of rest, although in the frog it is occasionally in the opposite direction (*Hermann*).

If the current be conducted uniformly from the **skin** of both hind feet of a cat, on stimulating the sciatic nerve of one side, not only is there a secretion of sweat (§ 288), but a secretion-current is developed (*Luchsinger and Hermann*). If two symmetrical parts of the skin in the leg or arm of a **man** be similarly tested, and the muscle of one side be contracted, a similar current is developed. Destruction or atrophy of the glands abolishes both the power of secretion and the secretion-current. There is no secretion-current from skin covered with hairs, but devoid of glands (*Bubnoff*). [The secretion-current from the **salivary glands**, *e.g.*, the submaxillary, is referred to in § 145 (*Bayliss and Bradford*).]

333. ELECTROTONIC CURRENTS IN NERVE AND MUSCLE.—[When a **constant current**, called the "**polarising current**," is passed through a stretch of nerve, the nerve is thrown into a peculiar condition, called the "electrotonic condition," or briefly **electrotonus**. In this condition the vital properties of the nerve are modified, *i.e.*—

(1) Its **electromotivity** (§ 333).
(2) Its **excitability** (§ 335).
(3) Its **conductivity** (§ 335).

The first is considered in this section, and the latter two in a subsequent section.]

1. **Positive Phase of Electrotonus.**—If a nerve be so arranged upon the electrodes (fig. 493, I) that its artificial transverse section lies on one, and its longitudinal on the other electrode, then the galvanometer indicates a strong current. If now a **constant current** be transmitted through the end of the nerve projecting beyond

the electrodes (the so-called "*polarising*" end of the nerve), and if the direction of this current *coincide* with that in the nerve, then the magnetic needle gives a greater deflection, indicating an *increase* of the nerve-current—"**the positive phase of electrotonus.**" The increase is greater the longer the stretch of nerve traversed by the current, the stronger the galvanic current, and the less the distance between the part of the nerve traversed by the constant current and that on the electrodes.

2. **Negative Phase of Electrotonus.**—If in the same length of nerve, the constant current passes in the **opposite** direction to the nerve-current (fig. 493, II), there is a diminution of the electro-motive force of the latter—"**negative phase of electrotonus.**"

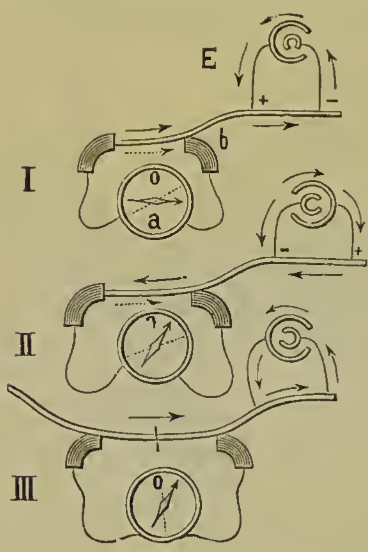


Fig. 493.
Nerve-current in electrotonus. *a*, galvanometer; *b*, electrodes; E, constant current.

3. **Equator.**—If two points of the nerve equi-distant from the equator be placed on the electrodes (III), there is no deflection of the galvanometer needle (p. 684, 4). If a constant current be passed through one free projecting end of the nerve, then the galvanometer indicates an electro-motive effect in the same direction as the constant current.

Electrotonus.—These experiments show that a constant current causes a change of the electromotive force of the part of the nerve directly traversed by the constant current, *i.e.*, in the intrapolar area, and also in the part of the nerve outside the electrodes, *i.e.*, in the extrapolar area. [The positive pole or the condition of anelectrotonus increases the electromotivity, while the negative pole or catheleetrotonus diminishes it, exactly the opposite of what obtains with the excitability.] This condition is called *electrotonus* (*du Bois-Reymond*, 1843).

The electrotonic current is strongest not far from the electrodes, and it may be twenty-five times as strong as the nerve-current of rest (§ 331, 5); it is greater on the anode than on the cathode side; it undergoes a negative variation like the resting nerve-current during tetanus; it occurs at once on closing the constant current, although it diminishes uninterruptedly at the cathode (*du Bois-Reymond*). On the contrary, between the electrodes, besides the polarising current itself, there is no obvious electrotonic increase of the current to be observed (*Hermann*). These phenomena take place only as long as the nerve is excitable. If the nerve be ligatured in the projecting part in the galvanometer circuit, the phenomena cease in the ligatured part. The above-described galvanic electrotonic changes of the extra-polar part are absent in non-medullated nerve-fibres, whilst, on the contrary, the physiological electrotonus is present. The physiological electrotonus of medullated nerves can be set aside by treating medullated nerves with ether, whilst the physical phenomena remain (*Biedermann*).

The negative variation (§ 332) occurs more rapidly than the electrotonic increase of the current, so that the former is over before the electro-motive increase occurs. The velocity of the electrotonic change in the current is less than the rapidity of propagation of the excitement in the nerves—being only 8 to 10 metres per second (*Tschirjew, Bernstein*).

"**The secondary contraction from a nerve**" depends upon the electrotonic state. If the sciatic nerve of a frog's nerve-muscle preparation be placed on an excised nerve, and if a constant current be passed through the free end of the latter—non-electrical stimuli being inactive—the muscles contract. This occurs because the electrotonising current in the excised nerve stimulates the nerve lying on it. By rapidly closing and opening the current, we obtain "*secondary tetanus from a nerve*" (p. 689).

[**Paradoxical Contraction.**—Exactly the same occurs when the current is applied to one of the two branches into which the sciatic nerve of the frog divides. The sciatic nerve of the frog divides at the lower end of the thigh into the *peroneal* and

tibial branches. If the sciatic nerve be divided above, and the peroneal branch be also divided and stimulated with the constant current, the muscles supplied by the tibial branch will contract. There is no contraction of the muscle if the peroneal nerve be ligatured.]

Polarising After-Currents.—When the constant current is opened, there are after-currents depending upon internal polarisation (§ 328). In *living* nerves, muscle, and electrical organs this internal polarisation current, when a strong primary current of very short duration is used, is always *positive*, *i.e.*, has the same direction as the primary current. Prolonged duration of the primary current ultimately causes negative polarisation. Between these two is a stage when there is no polarisation. Positive polarisation is especially strong in nerves when the primary current has the direction of the impulse in the nerve; in muscle, when the primary current is directed from the point of entrance of the nerve into the muscle towards the end of the muscle (§ 334, II.).

4. **Muscle-Current during Electrotonus.**—The constant current also produces an electrotonic condition in **muscle**; a constant current in the same direction increases the muscle-current, while one in an opposite direction weakens it, but the action is relatively feeble.

[**Electrotonic Phenomena in Conductors.**—Matteucci found that a metallic wire surrounded by a moist conductor, when traversed by a galvanic current, exhibits currents possessing the properties of electrotonic currents of nerves. He also found that the currents ceased if the wire was of zinc, and the envelope a saturated solution of zinc sulphate. This shows that these currents were due to polarisation between the core and the fluid. Hermann finds that the currents only obtain when a polarisable core is present. A straw without joints, if filled with a saturated solution of common salt, or the tentacles of a lobster when moistened with saline solution, and traversed by a constant current, exhibit similar electrotonic currents (*Hering*).]

[**Effect of Stimulation on the Polarisation of Nerve—I. During the flow of the polarising current.**—When a constant current is being passed through a piece of nerve stimulation of the nerve causes a positive variation of the current (*Grünhagen*, *Hermann*). This is due, not to a change in the resistance of the nerve, but probably to a change in the intensity of the excitatory process as it passes along the polarised nerve. When the cathode of the polarising current lies between the led-off area and the point of stimulation, the positive variation increases at first as the strength of the polarising current is increased, then diminishes, and finally, with a current which is not very strong, disappears. The nerve-impulse is, in fact, completely blocked by the cathode (*Hermann*).]

[If at this stage the nerve be stimulated in the intrapolar area, the positive variation can still be obtained. When the anode is next the point of stimulation, the stimulating electrodes being extrapolar, a limiting density of the polarising current can also be reached for which stimulation has no effect. This limit is far higher than for the cathode (*G. N. Stewart*).]

[When the extrapolar regions of a nerve through which a constant current is being passed are connected with a galvanometer, it is seen that on stimulation the electrotonic currents, both anodic and cathodic, undergo a negative variation (*Bernstein*). This is true only for current-densities below a certain limit. As the current is strengthened the negative variation on the anodic side gives place to a positive variation. This stage is reached with greater difficulty the greater is the distance between the region of the nerve led off to the galvanometer and the region traversed by the polarising current (*G. N. Stewart*).]

[**II. After the opening of the polarising current.**—When a voltaic current is passed through a nerve and the intrapolar region of the nerve connected with a galvanometer, immediately after the opening of the current the galvanometer may show, according to the strength of the current used and its time of closure, a deflection in the same direction as the current (positive polarisation deflection), or in the opposite direction (negative polarisation deflection), or a double deflection, first in the opposite, and then in the same direction (*du Bois-Reymond*).]

[If the nerve be stimulated as soon as the image has come to rest, there will be a movement in the opposite direction to the polarising current. Above a certain limit of current-density the effect is less when the excitation has to pass the anode than when it has to pass the cathode (*G. N. Stewart*).]

[When a voltaic current is passed through a nerve and the extrapolar regions connected with a galvanometer, immediately after the opening of the polarising current, the galvanometer indicates, in the case of the cathodic area, a deflection in the same direction as the polarising current; in the case of the anodic area a main deflection in the opposite direction, preceded under certain conditions by a smaller and more transitory deflection in the same direction.]

[When the anodic region is connected with the galvanometer, and the nerve is stimulated, the image moves in the direction of diminution of the main after-current. When the cathodic region is connected with the galvanometer the movement produced by stimulation is in the

direction of increase of the after-current, but where the polarising current has been closed only for a very short time it is in the opposite direction.]

[The electromotive effects of stimulation in polarised nerves may be all explained on the assumption that during the flow of the polarising current the conductivity for the nerve-impulse is less in the neighbourhood of the cathode than in the neighbourhood of the anode, and that after the opening of the current this relation is reversed. This assumption is borne out by the results of experiments on muscular contraction. When a fairly strong voltaic current is being passed through a nerve, stimulation of the middle point of the intrapolar region causes contraction more readily when the excitation has to pass the anode than when it has to pass the cathode. After the opening of the current the reverse is the case (*G. N. Stewart*).]

334. **THEORIES OF MUSCLE- AND NERVE-CURRENTS.—I. Molecular** or **pre-existence Theory.**—To explain the currents in muscle and nerve, du Bois-Reymond proposed the so-called molecular theory. According to this theory, a nerve or muscle-fibre is composed of a series of small electro-motive molecules arranged one behind the other, and surrounded by a conducting indifferent fluid. The molecules are supposed to have a positive equatorial zone directed towards the surface, and two negative polar surfaces directed towards the transverse section. Every fresh transverse section exposes new negative surfaces, and every artificial longitudinal section new positive areas.

This scheme explains the **strong currents,**—when the + longitudinal surface is connected with the – transverse surface, a current is obtained from the former to the latter,—but it does not explain the **feeble currents.** To explain their occurrence we must assume that, on the one hand, the electro-motive force of the molecules is weakened with varying rapidity at unequal distances from the equator; on the other, at unequal distances from the transverse section. Then, of course, differences of electrical potential obtain between the stronger and the feebler molecules.

Parelectronomy.—But the *natural* transverse section of a muscle, *i.e.*, the end of the tendon, is not negative, but more or less positive electrically. To explain this condition, du Bois-Reymond assumes that on the end of the tendon there is a layer of electro-positive muscle-substance. He supposes that each of the peripolar elements of muscle consists of two bipolar elements, and that a layer of this *half* element lies at the end of the tendon, so that its positive side is turned towards the free surface of the tendon. This layer he calls the "**parelectronomic layer.**" It is never completely absent. Sometimes it is so marked as to make the end of the tendon + in relation to the surface. Cauterisation destroys it. [It is supposed to be favoured by cold.]

The **negative variation** is explained by supposing that during the action of a muscle and nerve the electro-motive force of all the molecules is diminished. During partial contraction of a muscle, the contracted part assumes more the character of an indifferent conductor, which now becomes connected with the negative zone of the passive contents of the muscular fibres.

The electrotonic currents beyond the electrodes in nerves must be explained. To explain the electrotonic condition, it is assumed that the bipolar molecules are capable of rotation. The polarising current acts upon the direction of the molecules, so that they turn their negative surfaces towards the anode and their positive surfaces to the cathode, whereby the molecules of the intrapolar region have the arrangement of a Volta's pile. In the part of the nerve outside the electrodes, the further removed it is, the less precisely are the molecules arranged. Hence, the swing of the needle is less the further the extrapolar portion is from the electrodes.

II. Difference or **Alteration Theory.**—The difference theory was proposed by L. Hermann, and, according to him, the four following considerations are sufficient to explain the occurrence of the galvanic phenomena in living tissues:—(1) Protoplasm, by undergoing partial *death* in its continuity, whether by injury or by (horny or mucous) metamorphosis, becomes negative towards the uninjured part. (2) Protoplasm, by being partially *excited* in its continuity, becomes negative to the uninjured part. (3) Protoplasm, when partially *heated* in its continuity, becomes positive, and by cooling negative, to the unchanged part. (4) Protoplasm is strongly *polarisable* on its surface (muscle, nerve), the polarisation constants diminishing with excitement and in the process of dying.

Streamless Fresh Muscles.—It seems that passive, uninjured, and absolutely fresh nerves, and muscles, are completely devoid of a current, *e.g.*, the heart (*Engelmann*), also the musculature of fishes while still covered by the skin.

[According to Hermann, the currents obtained from muscle are due to injury of

the muscle-substance, whereby a difference of potential is set up, the injured part being negative to the uninjured. In fact, it is impossible to isolate a muscle without injuring it, owing to its connections. Frogs exhibit skin-currents after the skin is destroyed; the muscles still exhibit currents, but Hermann explains this by the action of the irritant, used to destroy the skin, also affecting the muscle. In **fishes**, however, there are no skin-currents, and if they be curarised, absolutely no current is obtained from their uninjured muscles (*Hermann*). The **heart** also when passive and uninjured gives no current, *i.e.*, it is iso-electrical although it exhibits an action-current when it contracts, and every injured part in it possesses a negative electrical potential with reference to the rest.]

L. Hermann also finds that the muscle-current is always developed after a time, which is very short, when a new transverse section is made. [By means of his "**Fall-rheotom**" an arrangement whereby a weight, covered with shagreen, injured a muscle, and at the same time closed and opened a galvanometer circuit, Hermann was able to show that the current—demarcation-current—took a certain time to develop. Had it been pre-existent, as supposed by du Bois-Reymond, this ought not to have been the case.]

Demarcation-Current.—Every **injury** of a muscle or nerve causes at the point of injury (*demarcation surface*) a dying substance, which behaves negatively to the positive intact substance. The current thus produced is called by Hermann the "*demarcation-current.*" If individual parts of a muscle be moistened with potash salts or muscle-juice, they become negatively electrical; if these substances be removed these parts cease to be negative (*Biedermann*).

It appears that all living protoplasmic substance has a special property, whereby injury of a part of it makes it, **when dying, negative**, while the intact parts remain positively electrical. Thus, all transverse sections of living parts of plants are negative to their surface (*Buff*); and the same occurs in animal parts, *e.g.*, glands and bones.

Engelmann made the remarkable observation that the **heart** and smooth muscle again lose the negative condition of their transverse section, when the muscle-cells are completely dead, as far as the cement-substance of the nearest cells; in nerves, when the divided portion dies, as far as the first node of Ranvier. When all these organs are again completely streamless, then the absolutely dead substance behaves essentially as an indifferent moist conductor. Muscles divided subcutaneously and healed do not exhibit a negative reaction of the surface of their section.

All these considerations go to show that *the pre-existence of a current in living uninjured tissues can no longer be maintained.*

Theoretical.—Grünhagen and L. Hermann explain the **electrotonic currents as** being due to **internal polarisation** in the nerve-fibre between the conducting core of the nerve and the enclosing sheaths. Matteucci found that, when a wire is surrounded with a moist conductor, and the covering placed in connection with the electrodes of a constant current, currents similar to the electrotonic currents in nerves, and due to polarisation, are developed. If either the wire or the moist covering be interrupted at any part, then the polarisation current does not extend beyond the rupture (p. 692). The polarisation developed on the surface of the wire by its transition-resistance causes the conducted current to extend much beyond the electrodes.

Muscles and nerves consist of fibres, surrounded by indifferent conductors. As soon as a constant current is closed, on their surface, internal polarisation is developed, which produces the electrotonic variation; it disappears again on opening or breaking the current. Polarisation is detected by the fact that, in living nerve, the galvanic resistance to conduction across a fibre is about five times, and in muscles about seven times, greater than in the longitudinal direction.

Action-Currents.—The term "**action-current**" is applied by L. Hermann to the currents obtained during the **activity of a muscle** or **nerve.** When a **single contraction-wave** passes along a muscular fibre, connected at two points with a galvanometer, then that point through which the wave is just passing is negative to the other. Occasionally, in excised muscles, local contractions occur, and these points are negative to the other passive parts of the muscle (*Biedermann*). In order, therefore, to explain the currents obtained from a frog's leg during **tetanus**, we must assume that the end of the fibre which is negative participates less in the excitement than the middle of the fibre. But this is the case only in dying or fatigued muscles.

According to § 336, D, the direct application of a constant current to a muscle causes contraction first at the cathode, when the current is closed, and when it is opened, at the anode. This is explained by assuming that, during the closing contraction, the muscle is negative at the cathode, while with the opening contraction the negative condition is at the anode.

If a **muscle** be thrown into contraction by stimulating its **nerve**, then the wave of excitement travels from the **entrance of the nerve** to both ends of the muscle, which also behave negatively to the passive parts of the muscle. According to the point at which the nerve enters the muscle the ascending or descending wave of excitement will reach the end (origin or insertion) of the muscle sooner than the other. On placing such a muscle in the galvanometer circuit, then at first that end of the muscle will be negative which lies nearest to the point of entrance of the nerve (*e.g.*, the upper end of the gastrocnemius), and afterwards the lower end. Thus, there appear rapidly after each other, at first a descending, and then an ascending—or **diphasic**—current in the galvanometer circuit, of course reversed within the muscle itself (*Sig. Mayer*) (§ 332, 4).

The same occurs in the muscles of the **human fore-arm**. When these were caused to contract through their **nerves**, at first the point of entrance of the nerve (10 cm. above the elbow-joint) was negative, and then followed the ends of the muscles when the contraction-wave, with a velocity of 10 to 13 metres per second, reached them (*L. Hermann*) (§ 399, 1).

If a completely uninjured, streamless muscle be made to contract *directly and in toto*, then neither during a single contraction, nor in tetanus, is there a current, because the whole of the muscle passes *at the same moment* into a condition of contraction.

Dying Nerve.—Hermann also supposes that the contents of dying and active nerves behave negatively to the passive normal portions.

Imbibition Currents.—When water flows through capillary spaces, this is accompanied by an electrical movement in the same direction (*Quincke, Zöllner*). Similarly, the forward movement of water in the capillary interspaces of non-living parts (pores of a porcelain plate) is also connected with electrical movements, which have the same direction as the current of water. The same effect occurs in the movement of water, which results in that condition known as *imbibition* of a body. We must remember that at the demarcation surface of an injured nerve or muscle imbibition takes place; that also at the contracted parts of a muscle imbibition of fluid occurs (§ 227, II.); and that during secretion there is a movement of the fluid particles.

In **plants**, electrical phenomena have been observed during the *passive* bending of vegetable parts (leaves or stalks), as well as during the *active* movements which are associated with the bending of certain parts, *e.g.*, as in the mimosa and dionæa (*Burdon-Sanderson*). These phenomena are perhaps explicable by the movement of water which must take place in the interior of the vegetable parts (*A. G. Kunkel*). The root-cap of a sprouting plant is negative to the seed coverings (*Hermann*); the cotyledons positive to the other parts of the seedling (*Müller-Hettlingen*). In the incubated hen's egg, the embryo is +, the yelk − (*Hermann and v. Gendre*).

335. ELECTRONIC ALTERATION OF THE EXCITABILITY.—Cause of Electrotonus.—If a certain stretch of a living nerve be traversed by a **constant** electrical or "**polarising**" **current**, it passes into a condition (*Ritter*, 1802, and others), which du Bois-Reymond called the electrotonic condition, for **electrotonus**, whereby its vital properties, including its **excitability, conductivity**, and **electromotivity** are modified. Here we shall consider the **electrotonic variation of the excitability.** This condition of **altered excitability** extends not only over the part actually traversed by the current, *i.e.*, the *intrapolar portion*, but it is communicated to the entire nerve, *i.e.*, to the extrapolar portions. Pflüger discovered the following laws of electrotonus:—

At the **positive pole** or *anode* the excitability is *diminished*—this is the region of **anelectrotonus**; at the **negative** pole or *cathode* (K) it is *increased*—this is the region of **cathelectrotonus.** The changes of excitability are most marked in the regions of the poles themselves (fig. 494, A).

Indifferent Point.—In the **intrapolar region** a point must exist where the anelectrotonic and cathelectrotonic regions meet, where therefore the excitability is unchanged; this is called the **indifference** or **neutral point.** This point lies nearer the anode (i) with a weak current, but with a strong current nearer the cathode (i''); hence, in the first case, almost the whole intrapolar portion is more excitable; in the latter, less excitable. [Expressed otherwise, a weak current increases the area over which the negative pole prevails, while the reverse is the case with a strong current. Or in the intrapolar region, the diminution of excita-

bility extends as the strength of the current increases, or to put it otherwise, with an increasing strength of current, the indifferent point moves from the positive to the negative pole.] Very strong currents greatly diminish the conductivity at the anode, and indeed may make the nerve *completely incapable of conduction* at this part.

At the cathode also, but only after the polarising current has passed for some time through the nerve (*Werigo*), the excitability is diminished, and the nerve in this area is rendered incapable of conduction (*Grünhagen*).

Extrapolar Region.—The extrapolar area, or that lying outside the electrodes, is greater the stronger the current. Further, with the weakest currents, the extrapolar anelectrotonic area is greater than the extrapolar cathelectrotonic. With strong currents this relation is reversed.

Fig. 494 shows the excitability of a nerve (*N*, *n*) traversed by a constant current in the direction of the arrow. The curve shows the degree of increased excitability in the neighbour-

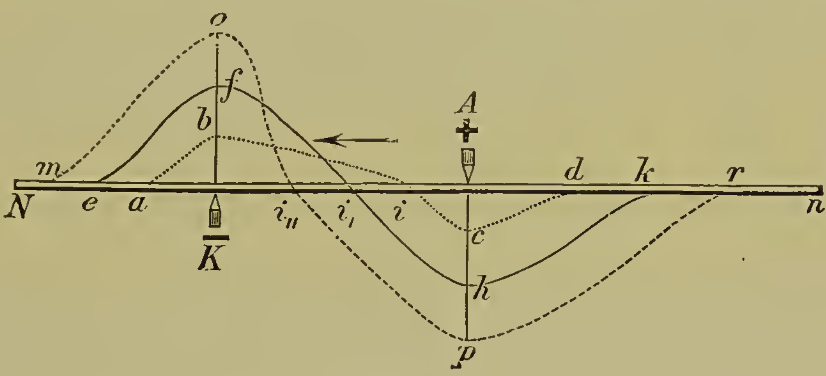


Fig. 494.

Scheme of the electrotonic excitability.

hood of the cathode (*K*) as an elevation above the nerve, diminution at the anode (*A*) as a depression. The curve *m*, *o*, *i''*, *p*, *r*, shows the degree of excitability with a strong current; *e*, *f*, *i'*, *h*, *k*, with a medium current; lastly, *a*, *b*, *i*, *c*, *d*, with a weak current.

The electrotonic effect increases with the length of the nerve traversed by the current. The changes of the excitability in electrotonus occur instantly when the circuit is closed, while anelectrotonus develops and extends more slowly. Cold diminishes electrotonus (*Hermann and v. Gendre*).

When the polarising current is opened or broken, at first there is a **reversal** of the relations of the excitability, and then there follows a transition to the normal condition of excitability of the passive nerve (*Pflüger*). At the very first moment of closing, Wundt observed that the excitability of the whole nerve was increased.

I. Proof of Electrotonus in Motor Nerves.—To test the laws of electrotonus, take a frog's nerve-muscle preparation (fig. 486). A constant current (p. 672) is applied to a limited part of the nerve by means of non-polarisable electrodes. A stimulus, electrical, chemical (saturated solution of common salt), or mechanical is applied either in the region of the anode or cathode; and we observe whether the contraction which results is greater when the polarising current is opened or closed. We shall consider the following cases (fig. 495).

(a) **Descending extrapolar anelectrotonus.** With a descending current we have to test the excitability of the extrapolar region at the anode. If the stimulus (common salt) applied at R (while the circuit was open) causes in this case (A) moderately strong contractions in the limb, then these at once become *weaker*, or *disappear* as soon as the constant current is transmitted through the nerve. After the circuit is opened, the contractions produced by the salt again occur of the original strength.

(b) **Descending extrapolar cathelectrotonus** (A). The stimulus (salt) is at R_1, and the contractions thereby produced are at once *increased* after closing the polarising current. On opening it they are again weakened.

(c) **Ascending extrapolar anelectrotonus** (B). The salt lies at r_1; the moderately strong contractions excited by the salt before the current is made become feebler after the current is made.

(d) **Ascending extrapolar cathelectrotonus** (B). The salt lies at r. In this case we must distinguish according to the *strength* of the polarising current:—(1) When the current is *very weak*, which can be obtained with the aid of the rheocord (fig. 458), on closing the polarising current, there is an *increase* of the contraction produced by salt. (2) If, however, the current is *stronger*, the contractions become either smaller or cease. This is due to the fact that with strong currents the conductivity of the nodes is diminished or even abolished (p. 697). Although the salt acts on the excitable nerve, there is no contraction of the muscle, as the conduction of an impulse is prevented by the resistance in the nerve.

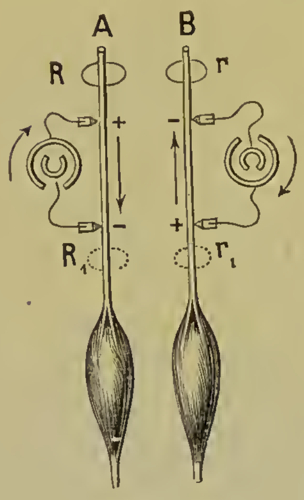


Fig. 495.

Method of testing the excitability in electrotonus. R, r, R_1, r_1, where the common salt (stimulus) is applied.

The **law of electrotonus** may also be **demonstrated** on a **completely isolated nerve.** The end of the nerve is properly disposed upon electrodes connected with a galvanometer, so as to obtain a *strong* nerve-current. If the nerve, when the constant current is closed, is stimulated in the anelectrotonic area, *e.g.*, by an induction shock, then the *negative variation is weaker* than when the polarising circuit was open. Conversely, it is stronger when it is stimulated in the cathelectrotonic area. The currents from the extrapolar areas of a nerve in a condition of electrotonus, exhibit the negative variation when the nerve is stimulated (*Bernstein*).

[Tigerstedt, instead of employing an electrical or chemical stimulus to excite the electrotonic nerve, used an apparatus like Heidenhain's tetanometer, whereby the nerve was beaten gently with a small ivory hammer. He fully confirms Pflüger's results.]

Proof in Man.—In performing this experiment it is important to remember the distribution of the current in the body. If both electrodes, for example, be placed over the course of the ulnar nerve (fig. 496), the currents entering the nerve at the anode (+ *a a*) must diminish the excitability; only above and below the anode (at *c c*) the positive current emerges from the nerve and excites cathelectrotonus at these points. Similarly, where the cathode is applied (− *c c*) there is increased excitability, but in higher and lower parts of the nerve, where (at *a a*) the positive current (coming from +) enters the nerve, the excitability is diminished (anelectrotonus) (*v. Helmholtz, Erb*). If we desire to stimulate in the neighbourhood of an electrode, then we cannot act upon that part of the nerve whose excitability is influenced by the electrode. In order, therefore, to stimulate *directly* the same point on which the electrode acts, it is necessary to apply the stimulus at the same time by the electrode itself, *e.g.*, either mechanically or by conducting the stimulating current through the polarising circuit (*Waller and de Watteville*).

II. **Proof of Electrotonus in Sensory Nerves.**—Isolate the sciatic nerve of a decapitated

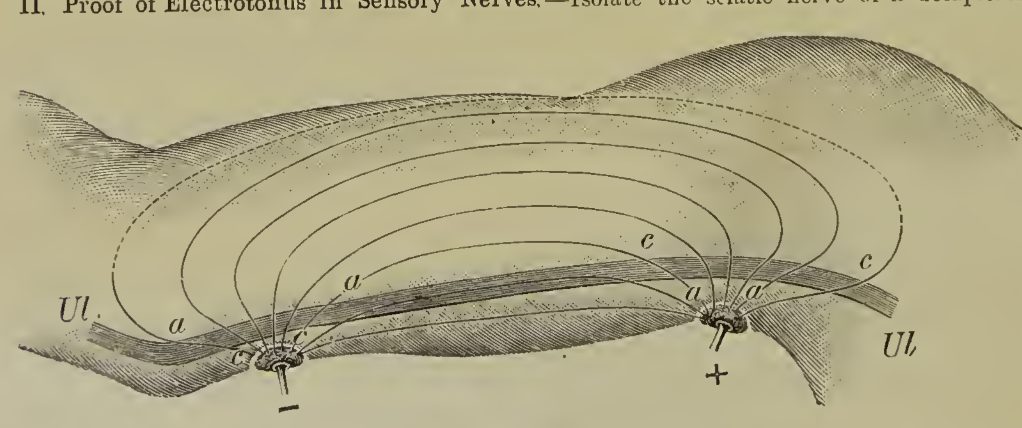


Fig. 496.

Scheme of the distribution of an electrical current in the nerve on galvanising the ulnar nerve.

frog. When this nerve is stimulated in its course with a saturated solution of common salt), *reflex movements* are excited in the other leg, the spinal cord being intact. These disappear as soon as a constant current is applied to the nerve, provided the salt lies in the anelectrotonic area (*Pflüger and Zurhelle, Hällstén*).

III. **Proof of Electrotonus in Inhibitory Nerves.**—To show this, proceed thus:—On causing dyspnœa in a rabbit, the number of heart-beats is diminished, owing to the action of the

dyspnœic blood on the cardio-inhibitory centre in the medulla oblongata. If, after dividing the vagus on one side, a constant descending current be passed through the other intact vagus, the number of pulse-beats is again increased (descending extrapolar anelectrotonus). If, however, the current through the nerve be an ascending one, then with *weak* currents the number of heart-beats increases still more (ascending extrapolar catelectrotonus). Hence, the action of inhibitory nerves in electrotonus is the opposite of that of motor nerves.

During the electrotonus of **muscle**, the excitability of the *intrapolar* portion is altered. The delay in the conduction is confined to this area alone (*v. Bezold*)—compare § 337, 1.

336. ELECTROTONUS—LAW OF CONTRACTION.—Opening and Closing Shocks.—A nerve is stimulated both at the moment of the occurrence and that of disappearance of electrotonus (*i.e.*, by closing and opening the current—*Ritter*):—(1) When the current is **closed**, the stimulation occurs only at the **cathode**, *i.e.*, at the moment when the catelectrotonus takes place (fig. 498). (2) When the current is **opened**, stimulation occurs only at the **anode**, *i.e.*, at the moment when the anelectrotonus disappears. [This is Pflüger's well-known principle—"*A given tract of nerve is stimulated by the appearance of catelectrotonus and the disappearance of anelectrotonus—not however by the disappearance of catelectrotonus nor by the appearance of anelectrotonus.*" From this principle can be deduced the so-called law of contraction.] (3) The stimulation at the occurrence of catelectrotonus is stronger than that at the disappearance of anelectrotonus (*Pflüger*).

Proof of stimulation at the anode at break. Ritter's Opening Tetanus.—That stimulation occurs only at the anode when the current is opened, *i.e.*, broken, was proved by Pflüger by means of "Ritter's opening tetanus." Ritter's tetanus consists in this, that when a constant current is passed for a long time through a long stretch of nerve, on opening the current, tetanus lasting for a considerable time results. If the current was a descending one [*i.e.*, with the − pole next the muscle], then this tetanus ceases at once after section of the intrapolar area, a proof that the tetanus resulted from the now separated anode. If the current was an ascending one [*i.e.*, with the + pole next the muscle], section of the nerve has no effect on the tetanus.

Proof of stimulation at the cathode at make.—Pflüger and v. Bezold found a further proof *that the closing or make contraction proceeds from the cathode, and the opening or break contraction from the anode*, by showing that with a **descending current**, the closing contraction in the muscle, at the moment of closing occurred *earlier*, while the opening contraction at the moment of opening occurred *later*; and, conversely, with an **ascending current** the closing contraction occurred later, and the opening contraction sooner. The difference in time corresponds to the time required for the propagation of the impulse in the intrapolar region (§ 337). If a large part of the intrapolar region in a frog's nerve be rendered inexcitable by applying ammonia to it, then only the electrode next the muscle stimulates, *i.e.*, always on closing or making a descending current and on opening or breaking an ascending one (*Biedermann*).

A. The law of contraction is valid for all kinds of nerves—**I.** The contraction occurring at the closing or opening of a constant current varies with—

(*a*) The **direction** (*Pfaff*), and
(*b*) The **strength** of the current (*Heidenhain*).

(1) **A weak current**, in conformity with the third of the above statements, causes only a **closing contraction, both with an ascending and a descending current.** The disappearance of electrotonus is so feeble a stimulus as not to excite the nerve.

(2) **A medium current** causes contractions at make and break, both with an ascending and a descending current.

(3) **A strong current** causes only a **closing contraction** with a **descending current**; there is no contraction at break, because with very strong currents almost the whole of the intrapolar portion of the electrotonic nerve is incapable of conducting an impulse (p. 697); an **ascending current** causes only a contraction at break for the same reason. With a certain strength of current, the muscle remains tetanic while the current is closed ("*closing tetanus*").

[The Pflüger's so-called **law of contraction** may be formulated as follows:—R = rest; C = contraction (fig. 497).]

Strength of Current.	Ascending.		Descending.	
	On Closing.	On Opening.	On Closing.	On Opening.
Weak, ...	C	R	C	R
Medium, ...	C	C	C	C
Strong, ...	R	C	C	R

II. In a **dying nerve**, losing its excitability, according to the Ritter-Valli law (§ 325, 7), the law of contraction is modified. In the stage of increased excitability, *weak* currents cause only closing contractions with both directions of the current. In the following stage, when the excitability begins to diminish, weak currents cause opening and closing contractions with both currents. Lastly, when the excitability is very greatly diminished, the descending current is followed only by a closing contraction, and the ascending by an opening contraction (*Ritter*, 1829).

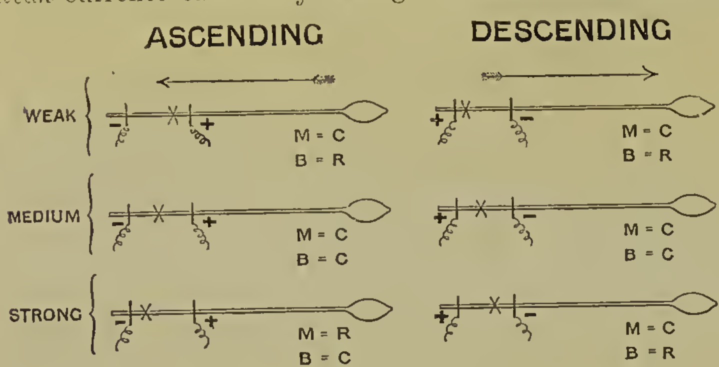


Fig. 497.

Scheme illustrating Pflüger's so-called law of contraction (*Stirling*).

III. As the various changes in excitability occur in a centrifugal direction along the nerve, we may detect the various stages simultaneously at different parts along the course of the nerve. According to Valentin and Fick, the living intact nerve shows only a closing contraction with both directions of the current, and opening contractions only with very strong currents.

Eckhard observed that, on opening an ascending medium current applied to the hypoglossal nerve of a rabbit, one-half of the tongue exhibited a *trembling* movement instead of a contraction, while on closing a descending current, the same result occurred (§ 297, 3).

According to Pflüger, we may represent to ourselves what happens as follows:—The molecules of the passive nerve are in a certain state of medium mobility. In **cathelectrotonus** the **mobility** of the molecules is **increased**, in **anelectrotonus** it is **diminished**. When the nerve-molecules pass from the condition of rest to a more mobile condition, *i.e.*, the appearance of cathelectrotonus; or when they pass from a more stable into a medium state of mobility, *i.e.*, the disappearance of anelectrotonus, each condition acts as a stimulus.

B. **The law for inhibitory nerves** is similar. Moleschott, v. Bezold, and Donders have found similar results for the vagus, with this difference, that, instead of the contraction of a muscle, there is inhibition of the heart.

C. **For sensory nerves** also the result is the same, but we must remember that the perceptive organ lies at the central end of the nerve, while in a motor nerve it is at the periphery (muscle). Pflüger studied the effect of closing and opening a current on sensory nerves by observing the **reflex movement** which resulted. *Weak* currents cause only closing contractions; *medium* currents both opening and closing contractions; *strong* descending currents only opening contractions; and ascending only closing contractions. *Weak* currents applied to the human *skin*

cause a sensation with both directions of the current only at closing; *strong descending* currents a sensation only at *opening*; strong *ascending* currents a sensation only at closing (*Marianini, Matteucci*). When the current is closed, there is prickly feeling, which increases with the strength of the current (*Volta*). Analogous phenomena have been observed in the **sense organs** (sensations of light and sound) by Volta and Ritter.

D. In **muscle**, the law of contraction is proved thus—by fixing one end of the muscle, keeping it tense, so that it cannot shorten, and opening and closing the current at this end. The end of the muscle, which is free to move, shows the same law of contraction as if the motor nerve were stimulated (*v. Bezold*). On closing the current, the contraction begins at the cathode; on opening at the anode (*Engelmann*).

[**Engelmann's Experiment.**—In order to demonstrate that, when a constant current is applied to a muscle, stimulation occurs only at the cathode when the current is made (closed) and at the anode when it is broken (opened), suspend a curarised sartorius of a frog (fig. 498, R), and pass through its upper end a constant current. On closing the current the contraction takes place at the cathode and the muscle contracts towards (C), but at break it contracts at the anode and turns towards (B).]

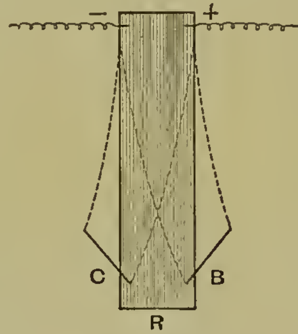


Fig. 498.
Scheme of Engelmann's experiment on the sartorius (R) of a frog.

E. Hering and Biedermann showed more clearly that *both the closing and opening contractions are purely polar effects*; when a *weak* current applied to a muscle is *made*, the first effect is a small contraction limited to the cathodic half of the muscle. Increase of the current causes increased contraction, which extends to the anode, but which is weaker there than at the cathode; at the same time, the muscle *remains contracted* during the time the current is made. At *break*, the contraction begins at the anode; even after breaking the current, the muscle for a time may remain contracted, which condition ceases on making the current in the same direction. The law of polar stimulation obtains in the case of **smooth muscle**, *e.g.*, in the excised uterus and intestines, in the cutaneous muscle of worms and holothurians. Most Rhizopoda show the reverse effect, viz., the anodic action on closing the current.

By killing the end of a muscle in various ways the excitability is diminished near this part. Hence, at such a place the polar action is feeble (*van Loon and Engelmann, Biedermann*). Touching a part with extract of flesh, potash, or alcohol diminishes locally the polar action, while soda salts and veratrin increase it (*Biedermann*).

Closing Continued Contraction.—The moderate continued contraction, which is sometimes observed in a muscle while the current is closed (fig. 400, Ö), depends upon the abnormal prolongation of the closing contraction of the cathode when a strong stimulus is used, or during the stage of dying, or in cooled winter frogs; sometimes the opening of the current is accompanied by a similar contraction proceeding from the anode (*Biedermann*). This tetanus is also due to the summation of a series of simple contractions (§ 298, III.). By acting on a muscle with a 2 per cent. saline solution containing sodic carbonate, the duration of the contraction is increased considerably, and occasionally the muscle contracts rhythmically (§ 296) (*Biedermann*).

If the whole muscle is placed in the circuit, the closing contraction is strongest with both directions of the current; during the time the circuit is closed, a continued contraction is strongest when the current is ascending (*Wundt*).

Inhibitory Polar Action on Muscle.—The constant current, when applied to a muscle in a condition of continued and sustained contraction, has exactly the opposite effect to that on a relaxed muscle. If by means of non-polarisable electrodes a constant current be sent through the long axis of a muscle in a state of

continued contraction, (*e.g.*, after poisoning with veratrin or through the contracted ventricle), when the current is made, it causes a **relaxation** beginning at the anode and extending to the other parts; on breaking the current applied to a muscle in continued contraction, the relaxation proceeds from the cathode.

Corresponding to this remarkable phenomenon, Biedermann found as regards the currents in the muscle-substance following the ordinary law, that every contracted part is negative to every passive section of the muscle. Perhaps the experiment of Pawlow, who found nerve-fibres in the adductor muscle of the mussel, whose stimulation caused relaxation of the muscular contraction, may throw some light on this question.

Ritter's Opening Tetanus.—If a nerve or muscle be traversed by a constant current for some time, we often obtain a prolonged **tetanus**, after opening the current (Ritter's **opening tetanus**, 1798). It is set aside by closing the original current, while closing a current in the opposite direction increases it ("**Volta's alternative**"). The continued passage of the current increases the excitability for the opening of the current in the same direction, and for the closing of the reverse current; conversely, it diminishes it for the closing of the current in the same direction, and for the opening of the reverse current (*Volta*).

According to Grützner and Tigerstedt, the cause of the opening contraction is partly due to the occurrence of polarising after-currents (§ 333), and according to Hermann to a diminution of the anodic positive polarisation.

Engelmann and Grünhagen explain the occurrence of opening and closing tetanus, thus, as due to latent stimulations, drying, variations of the temperature of the prepared nerves, which of themselves are too feeble to cause tetanus, but which become effective if an increased excitability obtains at the cathode after closure, and at the anode after opening the current.

Biedermann showed that, under certain conditions, two successive opening contractions can be obtained in a frog's nerve-muscle preparation, the second and later one corresponding to Ritter's tetanus. The first of these contractions is due to the disappearance of anelectrotonus in Pflüger's sense; the second is explained, like Ritter's opening tetanus, in Engelmann and Grünhagen's sense.

Simultaneous action of the constant current and the nerve-current.—Action of two currents. In a nerve-muscle preparation used to prove the law of contraction, of course a demarcation-current is developed in the nerve (§ 334, II.). If an artificial weak stimulating current be applied to such a nerve, we obtain an interference effect due to these two currents; closing a weak constant current causes a contraction, which, however, is not properly a closing contraction, but depends upon the opening (or derivation) of a branch of the demarcation-current; conversely, the opening of a weak constant current may excite a contraction, which is really due to the closing of a side branch of the nerve-current, in a secondary circuit through the electrodes (*Hering, Biedermann, Grützner*).

If two induction shocks be simultaneously applied to a motor nerve, two cases are possible. Either the one shock is so feeble that the nerve is not thereby sufficiently excited to cause a contraction, while the other shock causes only a feeble contraction. In this case, the sub-maximal shock plays the part of a weak constant current, and the size of the contraction depends only upon whether the effective stimulus was applied in the area of the anode or the cathode of the submaximal shock (*Sewall, Grünhagen, Werigo*). If, however, unequal, strong, induction shocks, each of which is effective—but separated from each other on account of the electrotonic action—be applied to an nerve, then the result is as if the stronger alone was active. The feebler wave of excitation passes completely into the stronger one (*Grünhagen, Werigo*).

337. TRANSMISSION OF NERVOUS IMPULSES.—1. If a **motor nerve** be stimulated at its central end (1) **a condition of excitation** is set up, and (2) an **impulse** is transmitted along the nerve to the muscle with a certain velocity. The latter depends on the former and represents the function of **conductivity**. The velocity is about 28 metres [about 90 feet] per second (*v. Helmholtz*), and for the human motor nerves 33·9 [100 to 120 feet per second] (*v. Helmholtz and Baxt*).

The velocity is less in the **visceral nerves**, *e.g.*, in the pharyngeal branches of the vagus 8·2 metres [26 feet] (*Chauveau*); in the motor nerves of the lobster 6 metres [18 feet] (*Fredericq and van de Velde*).

Modifying Conditions.—The velocity is influenced by various conditions:—**Temperature.**—It is lessened considerably by cold (*v. Helmholtz*), but both high

and low temperatures of the nerve (above or below 15° to 25° C.) lessen it (*Steiner and Trojtzky*), as also the action of **curare**, and the **electrotonic condition** (*v. Bezold*). The condition of anelectrotonus diminishes the velocity, while cath-electrotonus increases it (*Rutherford*, *Wundt*). It varies also with the **length** of the conducting nerve, but it increases with the **strength** of the stimulus (*v. Helmholtz and Baxt*), although not at first (*v. Vintschgau*).

Methods.—V. Helmholtz in 1850 estimated the velocity of the nerve-impulse in a frog's motor nerve by a method which is not now usually employed.

[The method now generally used is that shown in the scheme, fig. 499. Use a pendulum or **spring myograph** (fig. 323), and suspend in a suitable manner a frog's gastrocnemius (*m*), with a long portion of the sciatic nerve (N) dissected out, by fixing the femur in a clamp (*f*), while the tendo Achillis is fixed to a lever, which inscribes its movements on the smoked glass plate (P) of the myograph; place the **key** of the myograph (2) in the circuit with the battery (B), and the primary circuit of the induction machine (I). To the secondary coil (II), attach two wires, and connect them with a **commutator** *without cross-bars* (C). Connect the other binding screws of the commutator with two pairs of wires, arranged so that one pair can stimulate the nerve near the muscle (*a*) and the other at a distance from it (*b*). When the glass plate flies from one side to the other, the tooth (3) on its framework opens the key (2) in the primary circuit, and if the commutator be in the position

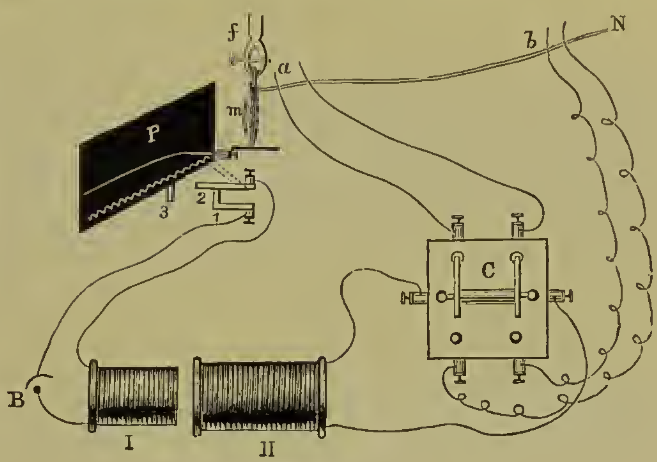


Fig. 499.

Scheme for measuring the velocity of nerve energy. *f*, clamp for femur; *m*, muscle; N, nerve; *a*, near, *b*, removed from C, commutator; II, secondary; I, primary spiral of induction machine B, battery; 1, 2, key; 3, tooth on the smoked plate.

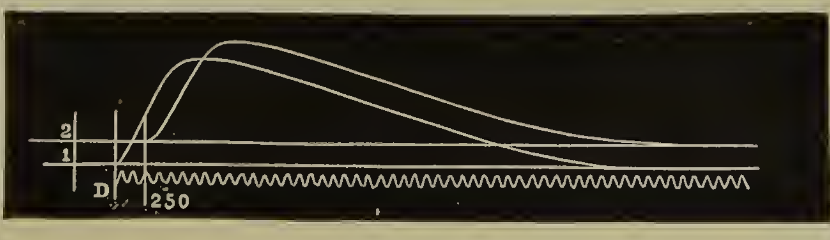


Fig. 500.

1, curve obtained on stimulating a nerve (man) near the muscle; 2, when the stimulus was applied to the nerve at a distance from the muscle; D, vibrations of a tuning-fork (250 per second).

indicated, then the induced current will stimulate the nerve at *a*, and a curve will be obtained on the glass plate. Rearrange the pendulum as before, *i.e.*, near the muscle, close the key in the primary circuit, but turn the handle of the commutator, and allow the glass plate to fly again.

This time the induced current will stimulate the nerve at *b*, *i.e.*, away from the muscle, and a second contraction, a *little later* than the first one, will be obtained. Register the velocity of the glass plate by means of a tuning-fork, and the curve

obtained will be something like fig. 500, although this curve was obtained on a cylinder travelling at a uniform rate, and the curves were drawn on abscissæ at different levels. The difference between the beginning of the *a* (1) and *b* (2) curves indicates the time that the nerve-impulse took to travel from *b* to *a*. This time is measured by the tuning-fork, and if the distance between the points *a* and *b* is known, then the calculation is a simple one. Suppose the stretch of nerve between *a* and *b* to be 2 inches, and the time required by the impulse to travel from *a* to *b* to be $\frac{1}{180}$ second, then we have the simple calculation—2 inches : 12 inches : : $\frac{1}{180}''$: $\frac{1}{80}''$, or 80 feet per second. In fig. 500 the experiment was made on **man**; the curve 1 was obtained by stimulating the nerve near the muscle, and 2 when the nerve was stimulated at a distance of 30 centimetres. The interval between the vertical lines corresponds to $\frac{1}{100}$ second, *i.e.*, the time required by the nerve-impulse to pass along 30 centimetres of nerve, which is equal to a velocity of 30 metres (90 feet) per second.]

In man, v. Helmholtz and Baxt estimated the velocity of the impulse in the **median nerve** by causing the muscles of the ball of the thumb to write off their contractions on a rapidly revolving cylinder. [In this case the "pince myographique" of Marey (fig. 409) may be used (§ 708). The ends of the pince are applied so as to embrace the ball of the thumb, so that when the muscles contract, the increase in *thickness* of the muscles expands the pince, which acts on a Marey's tambour, by which the movement is transmitted to another tambour provided with a writing-style, and inscribing its movements upon a rapidly moving surface, either rotatory or swinging.] The nerve is stimulated at one time in the axilla and again at the wrist. Two curves are obtained, which, of course, do not begin at the same time. The difference in time between the beginning of the two curves is the time taken by the impulse to traverse the above-mentioned length of nerve. [The time is easily ascertained by causing a tuning-fork of a known rate of vibration to write its movements under the curves.]

According to Bernstein, the stimulus which traverses the motor nerve to the end-plate and thus excites the muscle, must last on an average 0·0032 sec. (frog).

2. In the **sensory nerves of man**, the velocity of the impulse is probably about the same as in motor nerves. The rates given vary between 94 to 30 metres [280 to 90 feet] per second (*v. Helmholtz*).

Method of investigation.—Two points are chosen as far apart as possible, and at unequal distances from the brain, and they are successively excited by a momentary stimulus, *e.g.*, an opening induction shock applied successively to the tip of the ear and the great toe. The moment of the application of the stimulus is indicated on the registering surface. The person experimented on is provided with a key in connection with an electric arrangement, by which he can mark on the registering surface the moment he feels the sensation in each case (§ 374).

Pathological.—The conduction in the cutaneous nerves is sometimes greatly **delayed** in alterations of the cutaneous sensibility, in certain diseases of the spinal cord (§ 364). The sensation itself may be unchanged. Sometimes only the conduction for painful impressions is retarded, so that a painful impression on the skin is first perceived as a tactile sensation, and afterwards as pain, or conversely. When the interval of time between these two sensations is long, then there is a distinctly *double sensation* (*Naunyn*). It is rarely that voluntary movements are executed much more slowly from causes depending on the *motor* nerves, but occasionally the time between the voluntary impulse and the contraction is lengthened, but there may be in addition slower or longer continued contraction of the muscle. In tabes dorsalis or locomotor ataxia, the discharge of *reflex movements* is delayed; it is slower with thermal stimuli (60°) than with cold ones (0·5° C., *Ewald*).

338. DOUBLE CONDUCTION IN NERVES.—**Conductivity** is that property of a living nerve in virtue of which, on the application of a stimulus, it transmits an *impulse*. [The **nature of a nerve-impulse** is entirely unknown; we may conveniently term the process **nerve-motion**, but there is some reason to believe that nerve-energy is transmitted by some sort of molecular vibration.] The conductivity is **destroyed** by all influences or conditions which injure the nerve in its *continuity* (section, ligature, compression, destruction by chemical agents); or which abolish the *excitability* at any part of its course (absolute deprival of blood; certain drugs, *e.g.*, curare for the termination of motor nerves; also strong anelectrotonus, (§ 335). [If a motor nerve be ligatured, and then the nerve be stimulated above

the ligatured point, the muscle does not contract. The impulse requires integrity of the axis-cylinders in order to its conduction.]

[The following are the **laws of conduction** in a nerve :—

(1) There must be continuity and integrity of the nerve.
(2) The law of isolated conduction.
(3) There is double conduction in a nerve.
(4) The nerve-fibres possess independent excitability, and the result of stimulation depends on the structure in which the nerve-fibre ends. If the fibre ends in a muscle, the result is motion; if in a gland, secretion; in certain cells of the brain, sensation.]

[**Law of Isolated Conduction.**—Conduction always takes place only in the continuity of the fibres stimulated, the impulse never being transferred to adjoining nerve-fibres.]

Double Conduction in Nerves.—Although apparently conduction in motor nerves takes place only in a *centrifugal* direction towards the muscles, and in sensory nerves in a *centripetal* direction, *i.e.*, towards the centre, nevertheless, experiment has proved that a nerve conducts an impulse in *both* directions, just as in a non-living conductor. If a pure motor or sensory nerve be stimulated in its course, an impulse is propagated at the same time in a centrifugal and in a centripetal direction. This is the phenomenon of "*double conduction.*"

Proofs of Double Conduction.—1. If a nerve be stimulated, its **electro-motive properties** are affected both above and below the point of stimulation (see *Negative Variation in Nerves*, § 332).

2. **Electrical Nerves.**—If the posterior free end of the electrical centrifugal nerves of the malapterurus be stimulated, the branches given off above the point of stimulation are also excited, so that the whole electrical organ discharges its electricity (*Babuchin, Mantey*).

3. **Kühne's Experiments.**—(a) The **sartorius** of the frog has no nerve-fibres at its upper and lower ends. If the lower end be cut off, and if the lower third of the muscle be suspended and divided vertically, on stimulating mechanically one apex of the muscle, then the impulse passes in the motor nerves centripetally to the place where the nerve-fibre bifurcates in the muscle, and from thence centrifugally into the other or non-stimulated apex, and causes it to contract.

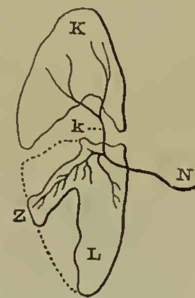


Fig. 501.
Kühne's Gracilis experiment.

[(*b*) The **Gracilis** of the frog is divided into a larger (L) and smaller portion (K) by a tendinous inscription running across it (fig. 501). The nerve (N) enters at the hilum in the larger portion, bifurcates, and gives a branch (*k*) to the smaller portion and another to the larger portion of the muscle. Let the muscle be cut as shown in fig. 501, avoiding injury to the nerves, so that only the nerve-twig (*k*) connects the larger and smaller portions of the muscle. If the tongue or tip of muscle (Z) with its nerves be stimulated, contraction occurs both in L and K, which is due to centripetal conduction in the motor nerve. The nerve-fibres divide dichotomously above where the nerves are given off to the portions L and K.]

[If the inscription be left, and the lower tip of the muscle (which is devoid of nerves) be stimulated, only the lower and not the upper part twitches; but if a part of the muscle containing nerves common to both parts be stimulated, then both parts of the muscle contract. This also proves that pure muscular excitation does not travel backwards from the muscle to the nerves. How this comes about we are entirely ignorant.]

The following experiments used to be cited as proofs, but they do not stand the test of criticism.

4. **Union of Motor and Sensory Nerves.**—If the hypoglossal and lingual nerves be divided in a dog, and if the peripheral end of the hypoglossal be stitched, so as to unite with the central end of the lingual (*Bidder*), then, several months after the union and restitution of the nerves, stimulation of the central end of the lingual causes contraction in the corresponding half of the tongue. Hence it has been assumed that the lingual, which is the *sensory* nerve of the tongue, must conduct the impulse in a peripheral direction to the end of the hypoglossal. This experiment is not conclusive, as the trunk of the lingual receives high up the centrifugal fibres from the seventh, viz., the chorda tympani, which may unite with or grow into the hypoglossal. Further, if the chorda be divided and allowed to degenerate before the above-described experiment is made, then no contractions occur on stimulating the lingual above the point of union (§ 349).

Fig. 502.
Double sponge rheophore.

Fig. 503.
Disc rheophore.

Fig. 504.
Metallic brush.

5. **Bert's Experiment.** — Paul Bert removed the skin from the tip of the *tail of a rat*, and stitched it into the skin of the back of the animal, where it united with the tissues. After the first union had taken place, the tail was then divided at its base, so that the tail, as it were, grew out of the skin on the back of the animal. On stimulating the tail, the animal exhibited signs of sensation. For the explanation of this experiment, see § 325.

339. **ELECTRO-THERAPEUTICS—REACTION OF DEGENERATION.**—Electricity is frequently employed for therapeutical purposes, the rapidly interrupted current of the induction machine, or **Faradic current**, being frequently used (especially since Duchenne, 1847), the *magneto-electrical* apparatus, and the *extra-current* apparatus. The **constant** or **galvanic current** is also used, especially since Remak's time, 1855 (§ 330).

I. **In paralysis,** *Faradic* currents are applied, either to the muscles themselves (*Duchenne*), or the points of entrance of the motor nerves, by means of suitable electrodes, or rheophores covered with sponge, &c., and moistened (*v. Ziemssen*).

[**Rheophores.**—Many different forms are used, according to the organ or part to be stimulated, or the effect desired. When electricity is applied to the skin to remove anæsthesia, hyperæsthesia, or altered sensibility, and we desire to limit the effect to the skin alone, then the rheophores are applied dry, and are usually made of metal. If, however, deeper-seated structures, as muscles or nerve-trunks, are to be affected, the skin must be well **moistened and** softened by sponging with warm water, while the rheophores are fitted with sponges moistened with common salt and water, which diminishes the resistance of the skin to the passage of electricity (figs. 502–504.]

In faradising the paralysed muscle, the object is to cause artificial movements in it, and thus prevent the degeneration which it would otherwise undergo, merely from inaction. If, in addition to the motor nerves, its *trophic* nerves are also paralysed, then a muscle atrophies, notwithstanding the faradisation (§ 325, 4). The use of the induced current also improves a paralysed muscle, as it increases the **blood-stream** through it, while it affects the **metabolism** of the muscle reflexly. In addition, weak currents may restore the excitability of enfeebled nerves (*v. Bezold, Engelmann*).

The figs. 504–508 indicate the positions of the motor points of the extremities, where, by stimulating at the entrance of the nerve, each muscle may be caused to contract singly. In § 349 the motor points of the face, and in § 347 those of the neck, are indicated.

The **constant** current may be employed as a stimulus, when it is closed and opened, in the form of an *interrupted* current, by altering its direction and increasing or diminishing its intensity, but it also causes a *polar action*. On *closing* the current, the nerve at the *cathode* is

stimulated; similarly, on *opening* the current, at the *anode* (§ 336). Thus, when the current is closed, the excitability of the nerve is increased at the cathode (§ 335), which may act

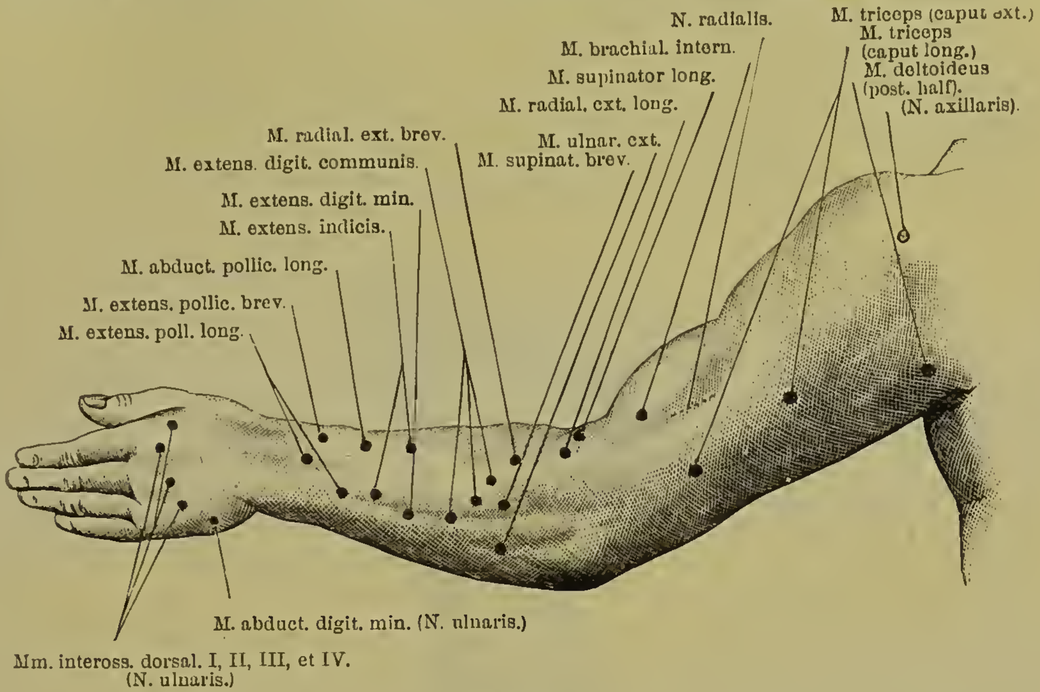


Fig. 505.

Motor points of the radial nerve and the muscles supplied by it; dorsal surface.

favourably upon the nerve. Increased excitability in electrotonus at the anode, although feebler, has been observed during percutaneous galvanisation in man. This is especially the

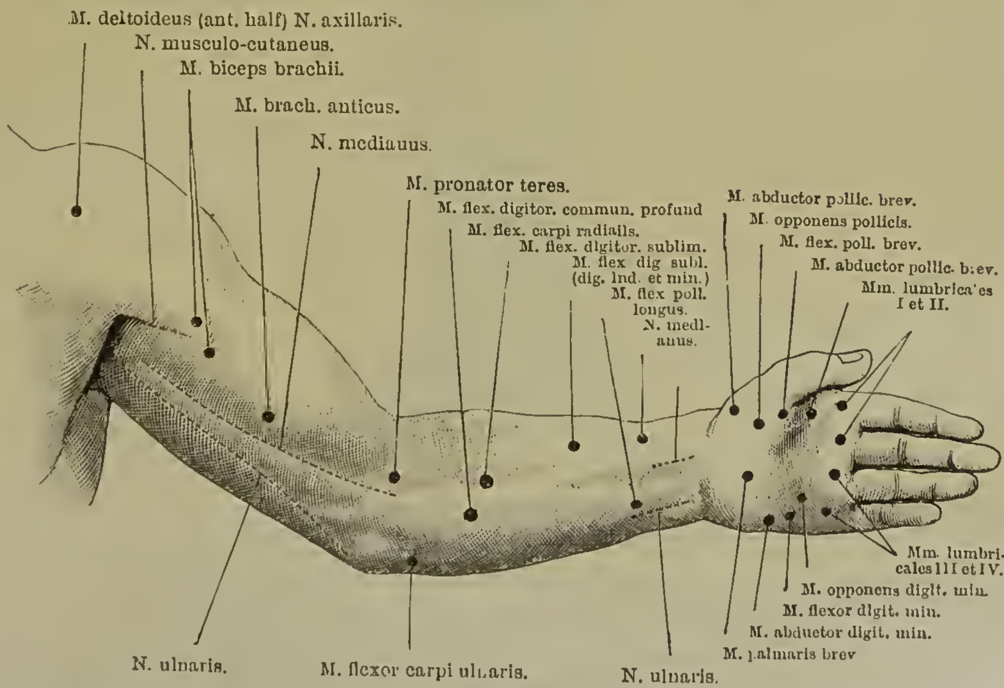


Fig. 506.

Motor points of the median and ulnar nerves, with the muscles supplied by them.

case by repeatedly reversing the current, sometimes also by opening and closing, or even with

a uniform current. If the increase of the excitability is obtained, then the direction of the current increases the excitability on closing the reverse current, and on opening the one in the same direction.

Restorative Effect of the Constant Current.—Further, in using the constant current, we have to consider its restorative effects, especially when it is *ascending*. R. Heidenhain found that feeble and fatigued muscles recover after the passage of a constant current through them.

Lastly, the constant current may be useful from its **catalytic** or **cataphoric** action (§ 328). The effect is directly upon the tissue elements. It may also act directly or reflexly upon the blood- and lymph-vessels.

Faradisation in Paralysis.—If the primary cause of the paralysis is in the muscles themselves, then the *induced* current is generally applied directly to the muscles themselves by means of

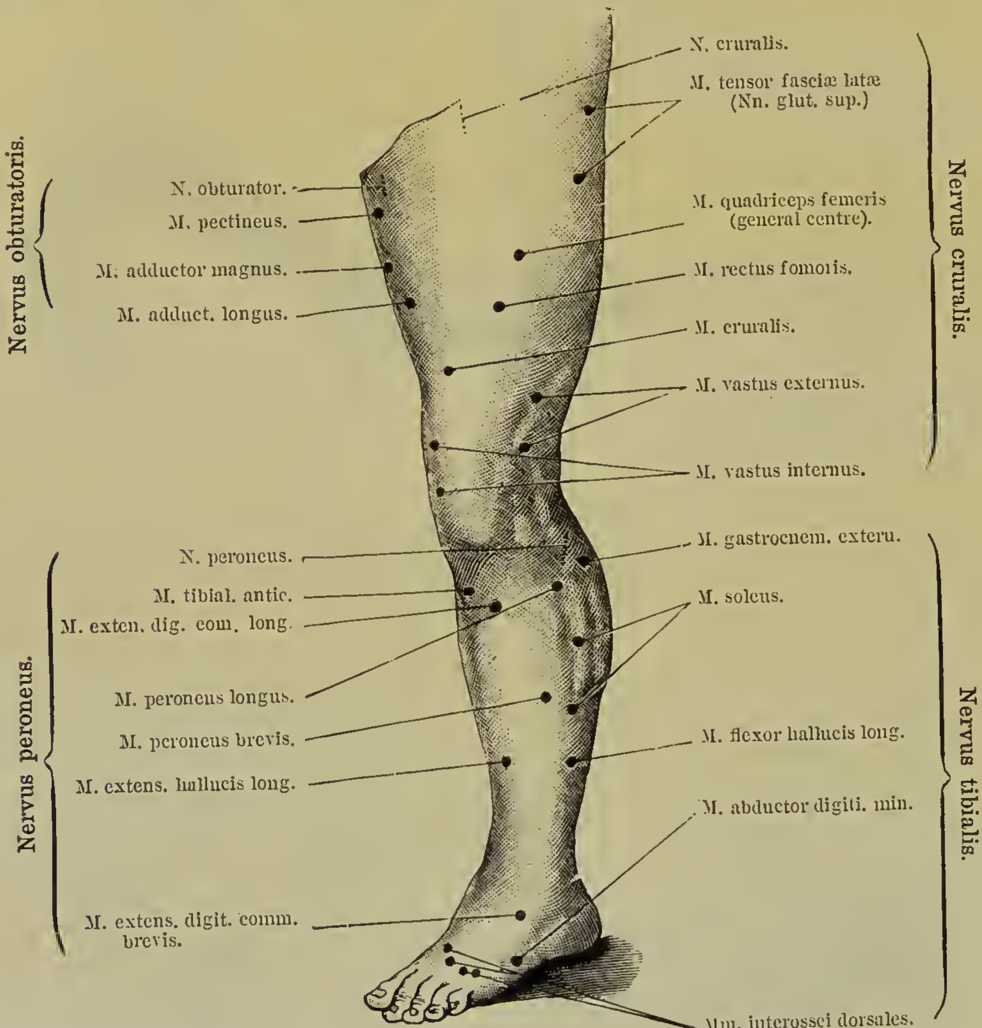


Fig. 507.

Motor points of the peroneal and tibial nerves on the front of the leg ; the peroneal on the left, the tibial on the right (after *Eichhorst*).

sponge electrodes (fig. 502) ; while, if the motor nerves are the primary seat, then the electrodes are applied over them. The current used must be only of *very moderate* strength ; strong tetanic contractions are injurious, and so is too prolonged application (*Eulenburg*).

The constant current may also be applied to the muscles or to their motor nerves, or to the centres of the latter, or to both muscle and nerve simultaneously. As a rule, the *cathode* is placed *nearer the centre*, as it increases the excitability. When the electrode is moved along the course of the nerve, or when the strength of the current is varied, the action is favoured. If the seat of the lesion is in the central nervous system, then the electrodes are applied along the vertebral column, or on the vertebral column, and the course of the nerves at the same

time, or one on the head and the other on a point as near as possible to the supposed seat of the lesion. The current must not be too strong nor applied too long.

Induced *v.* Constant Current: Reaction of Degeneration.—Paralysed nerves and muscles behave quite differently as regards the *induced* (rapidly interrupted) and the *constant* current. This is called the "**reaction of degeneration.**" We must remember the physiological fact that a *dying* nerve attached to a muscle (§ 325), and also the muscles of a curarised animal, react much less strongly to rapidly interrupted currents than fresh non-curarised muscles. Baierlacher, in 1859, found that, in a case of facial paralysis, the facial muscles contracted but feebly to the induced current, but very energetically on the constant current being used. The excitability for the constant current may be abnormally increased, but may disappear on recovery taking place. According to Neumann, it is the longer duration of the constant current as opposed to

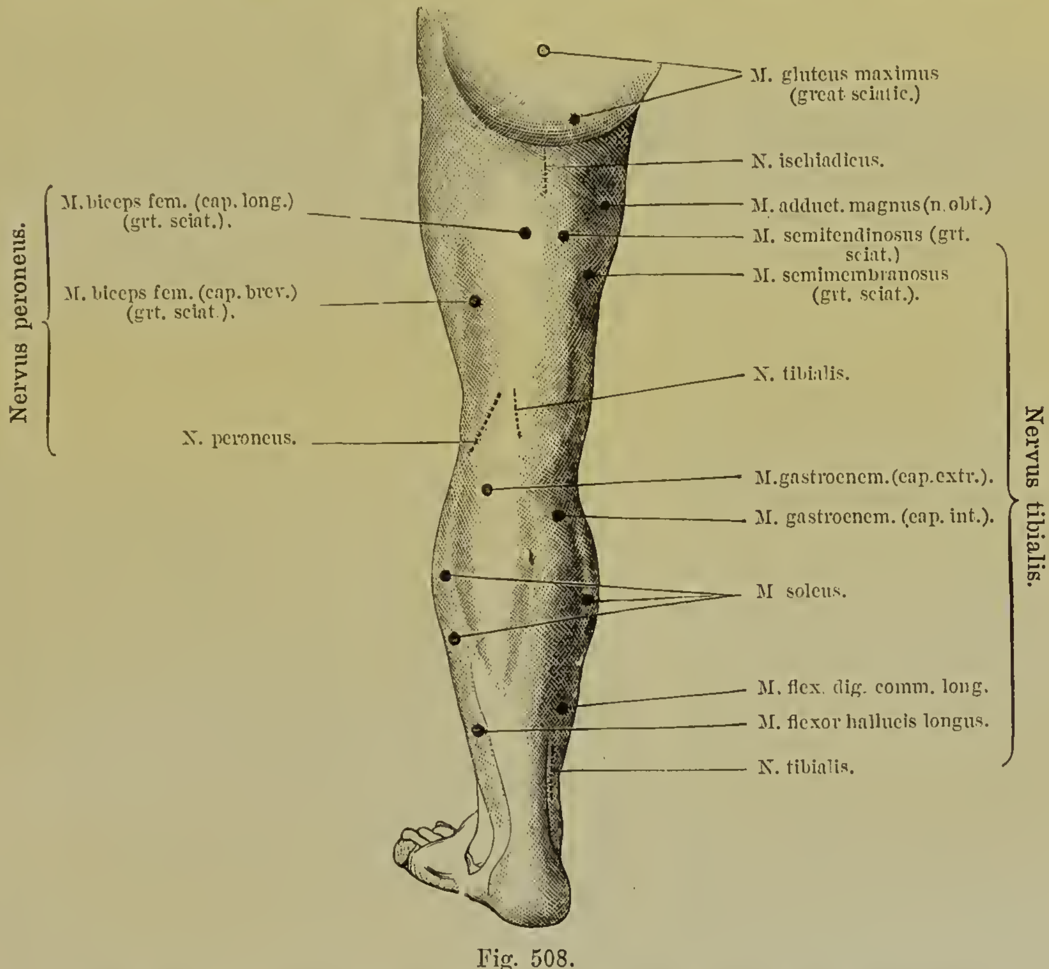


Fig. 508.

Motor points of the sciatic nerve and its branches; the peroneal and tibial nerves.

the momentary closing and opening of the induced current which makes the contraction of the muscle possible. If the constant current be broken as rapidly as the Faradic current is broken, then the constant current does not cause contraction. Conversely, the induced current may be rendered effective by causing it to last longer. We may also keep the primary circuit of the induction machine closed, and move the secondary spiral to and fro along the slots. Thus we obtain slow gradations of the induced current which act energetically upon curarised muscles (*Brücke*). Hence, in stimulating a muscle or nerve, we have to consider not only the **strength**, but also the **duration of the current**, just as the deflection of the magnetic needle depends upon these two factors.

[**Galvanic excitability** is the term applied to the condition of a nerve or muscle, whereby it responds to the opening or closing of a continuous current. The effects differ according as the current is opened or closed, and according to its strength. As a rule, the cathode causes a contraction chiefly at closure, the anode at opening the current, while the cathode is the stronger stimulus. With a *weak* current, the cathode produces a simple contraction on closing the current, but no contraction from the anode. With a *medium* current, we get with the cathode

a strong closing contraction but no opening contraction, while the anode excites feeble opening and closing contractions. With a *strong* current, we get with the cathode a tetanic contraction at closure, and a perceptible contraction at opening, while with the anode there is contraction both at opening and closing.]

[The law of contraction is usually expressed by the following formula (*Erb*):—An = anode, Ca = cathode, C = contraction, *c* = feeble contraction, C′ = strong contraction, S = closure of current, O = opening of current, Te = tetanic contraction—so that, expressing the above statements briefly, we have—

Weak currents produce Ca S C;
Medium ,, ,, Ca S C′, An S *c*, An O *c*;
Strong ,, ,, Ca S Te, An S C, An O C, Ca O*c*.]

[**Typical Reaction of Degeneration.**—When the reaction of the nerve and muscle to electrical stimulation is altered both **qualitatively** and **quantitatively**, we have the reaction of degeneration, which is characterised essentially by the following conditions:—The excitability of the *muscles* is diminished or abolished for the Faradic current, while it is increased for the galvanic current from the 3rd to 58th day; it again diminishes, however, with variations, from the 72nd to 80th day; the anode closing contraction is stronger than the cathode closing contraction. The contractions in the affected muscles occur slowly in a peristaltic manner, and are local, in contrast with the rapid contraction of normal muscle. The diminution of the excitability of the *nerves* is similar for the galvanic and Faradic currents. If the reaction of the nerves be normal while the muscle during direct stimulation with the constant current exhibits the reaction of degeneration, we speak of "**partial reaction of degeneration,**" which is constantly present in progressive muscular atrophy (*Erb*).

[The "**reaction of degeneration**" may occur before there is actual paralysis, as in lead poisoning. When it occurs we have to deal with some affection of the nerve-fibres, or of the trophic nerve-cells. When it is established, (1) stimulation of the nerve with Faradic or galvanic electricity does not cause contraction of the muscle; (2) direct Faradic stimulation of the muscles does not cause contraction; (3) the galvanic current usually excites contraction more readily than in a normal muscle, so that the muscle responds to much feebler currents than act on healthy muscles, but the contraction is longer and more of a tonic character, and shows a tendency to become tetanic. The electrical excitability is generally unaffected in paralysis of cerebral origin, and in some forms of spinal paralysis, as primary lateral sclerosis and transverse myelitis, but the "reaction of degeneration" occurs in traumatic paralysis, due to injury of the nerve-trunks, neuritis, rheumatic facial paralysis, lead palsy, and in affections of the nerve-cells in the anterior cornu of the grey matter of the spinal cord.] In rare cases the contraction of the muscles, caused by applying a *Faradic* current to the nerve, follows a slow peristaltic-like course—"*Faradic reaction of degeneration*" (*E. Remak, Erb*).

II. **In Various Forms of Spasm** (spasms, contracture, muscular tremor) the **constant current** is most effective (*Remak*). By the action of anelectrotonus, a pathological increase of the excitability is subdued. Hence, the anode ought to be applied to the part with increased excitability, and if it be a case of reflex spasm, to the points which are the origin or seat of the increased excitability. Weak currents of uniform intensity are most effective. The constant current may also be useful from its *cataphoric* action, whereby it favours the removal of irritants from the seat of the irritation. Further, the constant current increases the *voluntary control* over the affected muscles. In spasms of central origin, the constant current may be applied to the central organ itself. **Faradisation** is used in spasmodic affections to increase the vigour of enfeebled antagonistic muscles. Muscles in a condition of contracture are said to become more extensible under the influence of the Faradic current (*Remak*), as a normal muscle is more excitable during active contraction (§ 301).

In Cutaneous Anæsthesia, the *Faradic current* applied to the skin by means of hair-brush electrodes is frequently used (fig. 504). When using the *constant current*, the cathode must be applied to the parts with diminished sensibility. The constant current alone is applied to the *central* seat of the lesion, and care must be taken to what extent the occurrence of catheleetrotonus in the centre affects the occurrence of sensation.

III. **In Hyperæsthesia and Neuralgias,** Faradic currents are applied with the object of over-stimulating the hyper-sensitive parts, and thus to benumb them. Besides these powerful currents, *weak* currents act *reflexly* and accelerate the blood-stream, increase the heart's action, and constrict the blood-vessels, while *strong* currents cause the opposite effects (*O. Naumann*). Both may be useful. In employing the constant current in neuralgia (*Remak*), one object is by exciting anelectrotonus in the hyper-sensitive nerves, to cause a diminution of the excita-

bility. According to the nature of the case, the anode is placed either on the nerve-trunk, or even on the centre itself, and the cathode on an indifferent part of the body. The *catalytic* and *cataphoric* effects also are most important, for by means of them, especially in recent rheumatic neuralgias, the irritating inflammatory products are distributed and conducted away from the part. A descending current is transmitted continuously for a time through the nerve-trunk, and in recent cases its effects are sometimes very striking. Lastly, of course, the constant current may be used as a *cutaneous stimulus*, while the Faradic current also acts reflexly on the cardiac and vascular activity.

Recently, Charcot and Ballet have used the electric spark from an electrical machine in cases of anæsthesia, facial paralysis, and paralysis agitans. In some cases of spinal paralysis, muscles can be made to contract with the electric spark, which do not contract to a Faradic current. [Electricity is sometimes used to distinguish real from feigned disease, or to distinguish death from a condition of trance.]

Galvano-cautery.—The electrical current is used for *thermal* purposes, as in the galvano-cautery.

Galvano-Puncture.—The **electrolytic properties** of electrical currents are employed to cause coagulation in aneurisms or varix. [If the electrodes from a constant battery in action be inserted in an aneurismal sac, after a time the fibrin of the blood is deposited in the sac, whereby the cavity of the aneurism is gradually filled up. A galvanic current passed through defibrinated blood causes the formation of a coagulum of proteid matter at the positive pole and bubbles of gas at the negative (p. 463.)]

340. **ELECTRICAL CHARGING OF THE BODY.**—Saussure investigated by means of the electroscope the "charge" of a person standing on an insulated stool. The phenomena observed by him, which were always inconstant, were due to the *friction* of the clothes upon the skin. Gardini, Hemmer, Ahrens (1817), and Nasse regarded the body as normally charged with *positive* electricity, while Sjösten and others regarded it as *negatively* charged. Most probably all these phenomena are due to friction, and are modified effects of the air in contact with the heterogeneous clothing (*Hankel*). A strong charge resulting in an actual spark has frequently been described. Cardanus (1553) obtained sparks from the tips of the hair of the head. According to Horsford (1837), long sparks were obtained from the tips of the fingers of a nervous woman in Oxford, when she stood upon an insulated carpet. Sparks have often been observed on combing the hair, or stroking the back of a cat in the dark. Freshly voided *urine* is negatively electrical (*Vasalli-Eandi*, *Volta*); so is the freshly formed web of a spider, while the *blood* is positive.

341. **COMPARATIVE—HISTORICAL.**—**Electrical Fishes.**—Some of the most interesting phenomena connected with animal electricity are obtained in electrical fishes, of which there are about fifty species, including the electrical eel, or **Gymnotus electricus**, of the lagoons of the region of the Orinoco in South America—it may measure over 7 feet in length—the **Torpedo marmorata**, and some allied species, 30 to 70 centimetres [1 to 2½ feet], in the Adriatic and Mediterranean, the **Malapterurus electricus** or thunderer fish of the Arabs, a native of the Nile and the Niger, and the **Mormyrus**, allied to the pike, also of the Nile river. [**Rhinobatis electricus** of the Brazilian seas, and **Trichiurus electricus** of the Indian Ocean, and the **Raia batis**, or Skate of our own shores. Fifty species of fishes are believed to possess electrical organs.] By means of special **electrical organs** (*Redi*, 1666), these animals can in part voluntarily (gymnotus and malapterurus), and in part reflexly (torpedo), give a very powerful electrical shock. The electrical organ consists of "compartments" of various forms, separated from each other by connective-tissue, and filled with a jelly-like substance, which the nerves enter on one surface and ramify to produce a plexus. From this plexus there proceed branches of the axial cylinder, which end in a nucleated plate, the "**electrical plate**" (*Bilharz*, *M. Schültze*). When the "**electrical nerves**" proceeding to the organ are stimulated, an electrical discharge is the result.

Torpedo.—The electrical organs are two in number and lie immediately under the skin laterally on each side of the head, reaching as far as the pectoral fins. [Each electrical organ consists of about 800 hexagonal prisms placed vertically between the abdominal and dorsal integument, and separated from each other by membranous septa. Each prism is composed of about 600 plates, which are placed horizontally, and separated from each other by thin membranes. Thus there are about 1,000,000 electrical plates, each of which is supplied by a branch of a nerve-fibre.] Each nerve-fibre on reaching a prism divides, according to Wagner, into a "tuft" of fine nerve-fibrils, a fibril running to each plate in the column. The fibrils divide dichotomously in the plate, and the finer twigs anastomose with each other. The electric organs are developed from and replace the outer gill-muscles of the fifth gill arch. The electrical organs receive several nerves, which arise from the **lobus electricus** between the corpora quadrigemina and the medulla oblongata, and also branches from the trigeminus. The plates, which do not increase in number with the growth of the animal (*Delle Chiaje*, *Babuchin*), lie horizontally, while the nerve-fibres enter them on their dorsal surfaces, the current in the fish being from the abdominal to the dorsal surface (*Galvani*).

In **Malapterurus**, the organ surrounds the entire body, except the head and fins, like a mantle, and each half of it receives only one nerve-fibre (p. 654), whose axis-cylinder arises near the medulla oblongata from one gigantic ganglionic cell (*Bilharz*), and is composed of protoplasmic processes (*Fritsch*). The plates are also vertical, and receive their nerves from the posterior surface. The direction of the current is descending in the fish during the discharge (*du Bois-Reymond*).

In **Gymnotus**, the electrical organ consists of several rows of columns arranged along both sides of the spinal column of the animal under the skin as far as the tail. [There are four electrical organs, two on each side, stretching from the pectoral fins to near the tail.] It receives on the anterior surface several branches from the intercostal nerves. Besides this large organ there is a smaller one lying on both sides above the anal fins. Here the plates are vertical, and the direction of the electrical current in the fish is ascending, so that of course it is descending in the surrounding water (*Faraday, du Bois-Reymond*). [The plates arise from embryonic muscle. The nerve-cells from which the electrical nerves spring are arranged along the spinal cord, forming a special column.]

[In **Raia batis**, or the **Skate**, a fusiform electrical organ exists under the skin on each side of the tail (*Stark*), consisting of a number of longitudinal discs ; the discs are arranged in rows, and have one surface (flat) looking forwards, and the other backwards, showing a number of alveolar depressions. The anterior surface is covered with a nervous layer, into which numerous

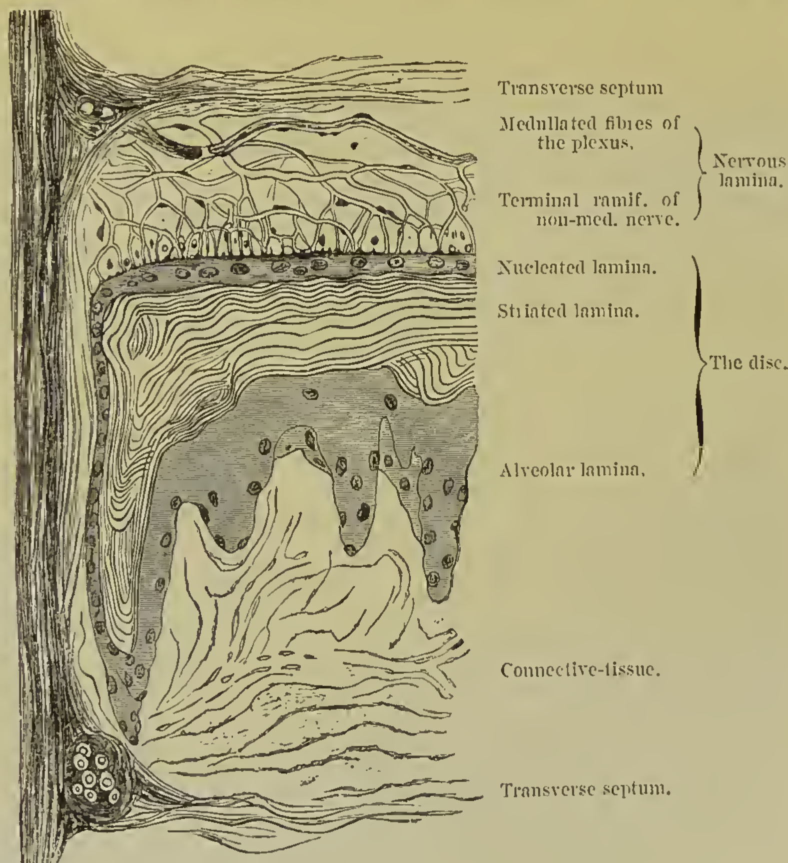


Fig. 509.

Vertical section of part of the electrical organ of a skate.

nerve-endings, showing dichotomous division, penetrate. It seems to correspond to the end-plate of muscles (fig. 509). The substance of the disc beneath the nervous or electric membrane consists of fine laminæ parallel to its surface.

It is extremely probable that the electric organs are **modified muscles**, in which the nerve-terminations are highly developed, the electrical plates corresponding to the motorial end-plates of the muscular fibres, the contractile substance having disappeared, so that during physiological activity the chemical energy is changed into electricity alone, while there is no " work " done. This view is supported by the observation of Babuchin, that during development the organs are originally formed like muscles ; further, that the organs when at rest are neutral, but when

active or dead, acid; and lastly, they contain a substance related to myosin which coagulates after death (§ 295—*Weyl*). The organs **manifest fatigue**; they have a "latent period" of 0·016 second, while one shock of the organ (comparable to the current in an active muscle) lasts 0·07 second. [Sanderson and Gotch found the latent period in curarised torpedos $= \frac{1}{100}$ sec.] About twenty-five of these shocks go to make a discharge, which lasts about 0·23 second. The discharge, like tetanus, is a discontinuous process (*Marey*). Mechanical, chemical, thermal, and electrical stimuli cause a discharge; a single induction shock is not effective (*Sachs*). During the electrical discharge the current traverses the muscles of the animal itself; the latter contract in the torpedo, while they do not do so in the gymnotus and malapterurus during the discharge (*Steiner*). A torpedo can give about fifty shocks per minute; it then becomes fatigued, and requires some time to recover itself. It may only partially discharge its organ (*Al. v. Humboldt*, *Sachs*). Cooling makes the organ less active, while heating it to 22° C. makes it more so. The organ becomes tetanic with strychnin (*Becquerel*), while curare paralyses it (*Sachs*). Stimulation of the electrical organ of the torpedo causes a discharge (*Matteucci*); cold retards it, while section of the electrical nerves paralyses the organ. The electrical fishes themselves are but slightly affected by very strong induction shocks transmitted through the water in which they are swimming (*du Bois-Reymond*). The substance of the electrical organs is singly refractive; excised portions give a current during rest, which has the same direction as the shock; tetanus of the organ weakens the current (*Sachs, du Bois-Reymond*). Perhaps the electrical organs of malapterurus is evolved from modified cutaneous glands (*Fritsch*).

[In the torpedo, the organ seems to be to a certain extent under the control of the will. Direct stimulation of the electric lobe causes a discharge in the electric organ of its own side; the organ may be discharged **reflexly** (*i.e.*, by stimulating any part of the animal's skin, and also **indirectly** by stimulating the electrical nerve passing to the organ. The "reflex discharge" consists of a succession of shocks. The discharge of an organ is comparable to tetanus of a muscle, and the individual shocks composing it to the single contractions that, when superposed, constitute tetanus. Curare has no effect on the excitation of the organ through its nerve (*Moreau*). According to Pacini the nerves are always distributed to the electric plate on the side which becomes negative in the discharge.]

Historical.—Richer (1672) made the first communication about the gymnotus. Walsh (1772) made investigations on the torpedo, on its discharge, and its power of communicating a shock. J. Davy magnetised particles of steel, caused a deflection of the magnetic needle, and obtained electrolysis with the electrical discharge. Becquerel, Brechet, and Matteucci studied the *direction* of the discharge. Al. v. Humboldt described the habits and actions of the gymnotus of South America. Hausen (1743) and de Sauvages (1744) supposed that electricity was the active force in nerves. The actual investigations into animal electricity began with G. Aloisio Galvani (1791), who observed that frogs' legs connected with an electrical machine contracted, and also when they were touched with two different metals. He believed that nerves and muscles generated electricity. Alessandro Volta ascribed the second experiment to the electrical current produced by the contact of dissimilar metals, and therefore outside the tissues of the frog. The contraction without metals described by Galvani was confirmed by Alex. v. Humboldt (1798). Pfaff (1793) first observed the effect of the direction of the current upon the contraction of a frog's leg obtained by stimulating its nerve. Bunzen made a galvanic pile of frogs' legs. The whole subject entered on a new phase with the construction of the galvanometer and since the introduction of the classical methods devised by du Bois-Reymond, *i.e.*, from 1843 onwards. [The more recent investigations on electrical organs have been made by Ranvier, Marey, Sanderson, Gotch and Ewart.]

Physiology of the Peripheral Nerves.

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342. **FUNCTIONAL CLASSIFICATION OF NERVE-FIBRES.**—As nerve-fibres, on being stimulated, are capable of conducting impulses in both directions (§ 338), it is obvious that the physiological position of a nerve-fibre must depend essentially upon its relations to the **peripheral end-organ** on the one hand, and its **central connection** on the other. Thus each nerve is distributed to a special area within which, under normal circumstances, in the intact body, it performs its functions. This function of the individual nerves, determined by their anatomical connections, is called their "specific energy." Nerve-fibres are classified as follows:—

I. Centrifugal or Efferent Nerves.

[Efferent fibres are those fibres that carry impulses from the centre, *i.e.*, the central nervous system, to the periphery.]

(a) Motor.—Those nerve-fibres whose peripheral end-organ consists of a **muscle**, the central ends of the fibres being connected with nerve-cells :—

1. Motor fibres of **striped muscle** (§§ 292–320).
2. Motor nerves of the **heart** (§ 57).
3. Motor nerves of **smooth muscle**, *e.g.*, the intestine (§ 171). The **vaso-motor** nerves are specially treated of in § 371.

(b) Secretory.—Those nerve-fibres whose peripheral end-organ consists of a **secretory cell**, the central ends of the fibres being connected with nerve-cells.

Examples of secretory nerves are the secretory nerves for saliva (§ 145), and those for sweating (§ 289, II.). [It is to be remembered, however, that these fibres not unfrequently lie in the same sheath with other nerve-fibres, so that stimulation of a nerve may give rise to several results, according to the kind of nerve-fibres present in the nerve. Thus, the secretory and vaso-motor nerves of glands may be excited simultaneously.]

(c) Trophic.—The end-organs of these nerve-fibres lie in the **tissues** themselves, and are as yet unknown. These nerves are called trophic, because they are supposed to govern or control the normal metabolism of the tissues.

In some tissues, we know of a direct connection of their elements with nerve-fibres, which may influence their nutrition. Nerves are connected with the corneal corpuscles (§ 201, 7), with the pigment-cells of the frog's skin (*Ehrmann*), the connective-tissue corpuscles of the serous membrane of the stomach of the frog, and the cells around the stomata of lymphatic surfaces (§ 196, 5) (*E. F. Hoffmann*).

Trophic Influence of Nerves.—The trophic functions of certain nerves are referred to as under :—On the influence of the **trigeminus** on the eye, the mucous membrane of the mouth and nose, the **face** (§ 347) ; the influence of the **vagus** on the **lungs** (§ 352) ; **motor nerves** on **muscle** (§ 307) ; **nerve-centres** on **nerve-fibres** (§ 325, 4) ; certain **central organs** upon certain **viscera** (§ 379).

Section of certain nerves influences the growth of the **bones**. H. Nasse found that, after section of their nerves, the bones showed an absolute diminution of all their individual constituents, while there was an increase of the fat. Section of the spermatic nerve is followed by degeneration of the testicle (*Nélaton, Obolensky*). After extirpation of their secretory nerves,

there is degeneration of the sub-maxillary glands (p. 249). Section of the nerves of the cock's-comb interferes with the nutrition of that organ (*Legros, Schiff*). After section of the 2nd cervical nerve in rabbits and cats, the hair falls off the ear on that side (*Joseph*). Section of the cervical sympathetic nerve in *young, growing* animals is followed by a more rapid growth of the ear upon that side (*Bidder, Stirling, Stricker*), also of the hair on that side (*Schiff, Stirling*); while it is said that the corresponding half of the brain is smaller, which, perhaps, is due to the pressure from the dilated blood-vessels (*Brown-Séquard*).

Blood-Vessels.—Lewaschew found that prolonged uninterrupted stimulation of the sciatic nerve of dogs, by means of chemical stimuli [threads dipped in sulphuric acid], caused hypertrophy of the lower limb and foot, together with the formation of aneurismal dilatations upon the blood-vessels.

Skin and Cutaneous Appendages.—In man, stimulation or paralysis of nerves, or degeneration of the grey matter of the spinal cord, is not unfrequently followed by changes in the pigmentation of the skin, in the nails, in the hair and its mode of growth and colour (*Jarisch*). [Injury to the brain, as by a fall, sometimes results in paralysis of the hair-follicles, so that, after such an injury, the hair is lost over nearly the whole of the body.] Sometimes there may be eruptions upon the skin, apparently traumatic in their origin (*v. Barensprung*). Sometimes there is a tendency to decubitus (§ 379), and in some rare cases of tabes, there is a peculiar degeneration of the joints (**Charcot's disease**). The changes which take place in a nerve separated from its centre are described in § 325.

[**Trophoneuroses.**—Some of the chief data on which the existence of trophic nerves is assumed are indicated above. There are many pathological conditions referable to diseases or injuries of nerves.]

[**Muscles.**—As is well known, paralysis of a motor nerve leads to simple atrophy of the corresponding muscle, provided it be not exercised; but when the motor ganglionic cells of the anterior horn of grey matter, or the corresponding cells in the crus, pons, and medulla, are destroyed, there is an active condition of atrophy with proliferation of the muscular nuclei. **Progressive muscular atrophy**, or wasting palsy, is another trophic change in muscle, whereby either individual muscles, or groups of muscles, are one after the other paralysed and become atrophied. In **pseudo-hypertrophic paralysis**, there is cirrhosis or increased development of the connective-tissue, with a diminution of the true muscular elements, so that although the muscles increase in bulk their power is diminished.]

[**Cutaneous Trophic Affections.**—Amongst these may be mentioned the occurrence of red patches or erythema, urticaria or nettle-rash, some forms of lichen, eczema, the bullæ or blebs of pemphigus, and some forms of ichthyosis, each of which may occur in limited areas after injury to a nerve or its spinal or cerebral centre. The relation between the cutaneous eruption and the distribution of a nerve is sometimes very marked in **herpes zoster**, which frequently follows the distribution of the intercostal and supraorbital nerves. **Glossy skin** (*Paget, Weir Mitchell*) is a condition depending upon impaired nutrition and circulation, and due to injuries of nerves. The skin is smooth and glossy in the area of distribution of certain nerves, while the wrinkles and folds have disappeared. In **myxœdema**, the subcutaneous tissue and other organs are infiltrated with, while the blood contains, *mucin*. The subcutaneous tissue is swollen, and the patient looks as if suffering from renal dropsy. There is marked alteration of the cerebral faculties, and a condition resembling a "cretinoid state" such as occurs after the excision of the thyroid gland. Victor Horsley has shown that a similar condition occurs in monkeys after excision of the thyroid gland (§ 103, III.). Laycock described a condition of **nervous œdema** which occurs in some cases of hemiplegia, and apparently it is independent of renal or cardiac disease.]

[There are alterations in the **colour** of the skin depending on nervous affections, including localised **leucoderma**, where circumscribed patches of the skin are devoid of pigment. The pigmentation of the skin in **Addison's disease** or **bronzed skin**, which occurs in some cases of disease of the suprarenal capsules, may be partly nervous in its origin, more especially when we consider the remarkable pigmentation that occurs around the nipple and some other parts of the body during pregnancy, and in some uterine and ovarian affections.

In **anæsthetic leprosy**, the anæsthesia is due to the disease of the nervous structure, which results in disturbance of motion and nutrition. Amongst other remarkable changes in the skin, perhaps due to trophic conditions, are those of symmetrical and local *gangrene*, and **acute decubitus** or bed-sores.]

[**Bed-Sores.**—Besides the simple chronic form, which results from over-pressure, bad nursing, and inattention to cleanliness, combined with some defect of the nervous conditions, there is another form, **acute decubitus**, which is due directly to nerve influence (*Charcot*). The latter usually appears within a few hours or days of the cerebral or spinal lesion, and the whole cycle of changes—from the appearance of the erythematous dusky patch to inflammation, ulceration, and gangrene of the buttock—is completed in a few days. An acute bed-sore may form when every attention is paid to the avoidance of pressure and other unfavourable conditions. When it depends on cerebral affections, it begins and develops rapidly in the centre of the gluteal region on the paralysed side, but when it is due to disease of the spinal cord it forms

more in the middle line in the sacral region; while in unilateral spinal lesions it occurs not on the paralysed, but on the anæsthetic side, a fact which seems to show that the trophic, like the sensory fibres, decussate in the cord (*Ross*).]

[There are other forms due to nervous disease, including **symmetrical gangrene** and local asphyxia of the terminal parts of the body, such as toes, nose, and external ear, caused perhaps by spasm of the small arterioles (**Raynaud's disease**); and the still more curious condition of **perforating ulcer of the foot.** Hæmorrhage of nervous origin sometimes occurs in the skin, including those that occur in locomotor ataxia after severe attacks of pain, and **hæmatoma aurium**, or the insane ear, which is specially common in general paralytics.]

(d) [**Inhibitory nerves** are those nerves which modify, inhibit, or suppress a motor or secretory act already in progress.]

Take as an **example** the effect of the **vagus** upon the action of the **heart**. Stimulation of the peripheral end of the vagus causes the heart to stand still in diastole (§ 85); see also the effect of the **splanchnic** upon the **intestinal movements** (§ 161). The **vaso-dilator** nerves, or those whose stimulation is followed by dilatation of the **blood-vessels** of the area which they supply, are referred to especially in § 237.

[There is the greatest uncertainty as to the **nature and mode of action of inhibitory nerves**, but take as a type the **vagus** which depresses the function of the heart, as shown by the slower rhythm, diminution of the contractions, relaxation of the muscular tissue, lowering of the excitability and conduction. These phenomena are not due to exhaustion. Gaskell points out that the action is beneficial in its after-effects, so that this nerve, although it causes diminished activity, is followed by repair of function; hence, he groups it as an **anabolic nerve**, the outward symptoms of cessation of function indicating that constructive chemical changes are going on in the tissue.]

(e) **Thermic and electrical nerves** have also been surmised to exist.

[Gaskell classifies the **efferent nerves** differently. Besides **motor nerves** to striped muscle, he groups them as follows:—

1. Nerves to **vascular muscles.**
   - (*a*) *Vaso-motor, i.e.*, vaso-constrictors; accelerators and augmentors of the heart.
   - (*b*) *Vaso-inhibitory, i.e.*, vaso-dilators; and inhibitors of the heart.
2. Nerves of the **visceral muscles.**
   - (*a*) *Viscero-motor.*
   - (*b*) *Viscero-inhibitory.*
3. **Glandular nerves.**]

[Other terms are applied to nerves with reference to the **chemical changes** they excite in a tissue in which they terminate. The ordinary metabolism is the resultant of two processes—one constructive, the other destructive, or of assimilation and dissimilation respectively. The former process is anabolism, the latter katabolism. A motor nerve excites chemical destructive changes in a muscle, and is so far the **katabolic nerve** of that tissue; secretory nerves are also katabolic in this sense; in the same way the sympathetic to the heart, by causing more rapid contraction, is also a katabolic nerve, while the vagus, as it arrests the heart's action, and brings about a constructive metabolism of the cardiac tissue, is an **anabolic nerve**, and so are the inhibitory nerves of the blood-vessels and the viscera (*Gaskell*).]

II. Centripetal or Afferent Nerves.

[Afferent nerve-fibres are those fibres that carry impulses from the periphery to the centre, usually the central nervous system.]

(a) **Sensory nerves** (sensory in the narrower sense), which by means of special end-organs conduct sensory impulses to the central nervous system.

(b) **Nerves of Special Sense.**

(c) **Reflex or Excito-motor Nerves.**—When the periphery of one of these nerves is stimulated, an impulse is set up which is conducted by them to a nerve-centre, from whence it is transferred to a *centrifugal* or *efferent* fibre, and the mechanism (I, a, b, c, d) in connection with the peripheral end of this efferent fibre is set in action; thus there are—**Reflex motor, Reflex secretory,** and **Reflex inhibitory**

fibres. [Fig. 510 shows the simplest mechanism necessary for a reflex motor act. The impulse starts from the skin, S, travels up the nerve, *af*, to the nerve-centre or nerve-cell, N, situate it may be in the spinal cord, where it is modified and transferred to the outgoing fibre, *ef*, and conveyed by it to the muscle, M.]

[In all probability the mechanism is not so simple as is shown in fig. 510. In some cases both the ingoing and the outgoing fibres are connected with separate nerve-cells, so that the fig. 511 would represent what occurs in this case. Fig. 511 represents, on the same hypothesis, schemata of a reflex secretory act, and also of a reflex inhibitory act. In the last case, the impulses carried along the fibre, *inh*, prevent the reflex motor effect from taking place.]

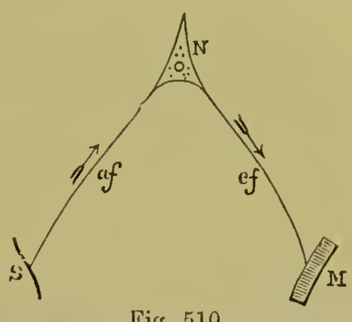


Fig. 510.

Scheme of a reflex motor act. S, skin; *af*, afferent nerve; N, nerve-cell; *ef*, efferent fibre.

Reflex motor. Reflex sensory. Reflex inhibitory.

Fig. 511.

Schemata of various reflex acts (*Stirling*).

III. Intercentral Nerves.

These fibres serve to connect ganglionic centres with each other, as, for example, in co-ordinated movements, and in extensive reflex acts.

THE CRANIAL NERVES.

343. I. **NERVUS OLFACTORIUS.**—**Anatomical.**—The three-sided prismatic **tractus olfactorius**, lying in a groove on the under surface of the frontal lobe, arises by means of an inner, outer, and middle root, from the tuber olfactorium (fig. 428, I). The tractus swells out upon the cribriform plate of the ethmoid bone, and becomes the **bulbus olfactorius**, which is the analogue of the special portion of the brain, existing in different mammals with a well-developed sense of smell (*Gratiolet*). From twelve to fifteen olfactory filaments pass through the foramina in the cribriform plate of the ethmoid bone. At first they lie between the periosteum and the mucous membrane, but in the lower third of their course they enter the mucous membrane of the regio olfactoria. The bulb consists of white matter below, and above of grey matter mixed with small spindle-shaped ganglionic cells (§ 420). Henle describes six, and Meynert eight layers, of nervous matter seen on transverse section. [The **centre for smell** lies in the tip of the uncinate gyrus on the inner surface of the cerebral hemisphere (*Ferrier*).] According to Gudden, removal of the olfactory bulb is followed by atrophy of the gyrus uncinatus on the same side. According to Hill, the three roots of the olfactory bulb stream backwards, the inner one is small, the middle one is a thick bundle, which grooves the head of the caudate nucleus, curves inwards to the anterior commissure, and crosses *vid* this commissure where it decussates, and passes to the extremity of the temporo-sphenoidal lobe. The outer roots pass transversely into the pyriform lobe, thence *vid* the fornix, corpora albicantia, the bundle of Vicq d'Azyr into the anterior end of the optic thalamus. Hill also points out that the elements contained in the olfactory bulb are identical with those contained in the four outer layers of the retina. Flechsig traces its origin (1) to the gyrus fornicatus, (2) through the lamina perforata anterior to the internal capsule (sensory part), and to the gyrus uncinatus (sensory

area of the cerebrum) (§ 378, IV.). Probably the fibres at their origin cross to the cerebrum. There is a connection between the olfactory bulbs in the anterior commissure. [Each nerve is related to both hemispheres.]

Function.—It is the only **nerve of smell**. Physiologically, it is excited only by gaseous odorous bodies—(*Sense of Smell*, § 420). Stimulation of the nerve, by any other form of stimulus, in any part of its course, causes a sensation of smell. [It also conveys those impressions which we call flavours, but in this case the sensation is combined with impressions from the organs of taste. In this case also the stimulus reaches the nerve by the posterior nares.] Congenital absence or section of both olfactory nerves abolishes the sense of smell (easily performed on young animals—*Biffi*).

Pathological.—The term **hyperosmia** is applied to cases where the sense of smell is excessively and abnormally acute, as in some hysterical persons, and in cases where there is a purely subjective sense of smell, as in some insane persons. The latter is perhaps due to an abnormal stimulation of the cortical centre (§ 378, IV.). **Hyposmia** and **anosmia** (*i.e.*, diminution and abolition of the sense of smell) may be due to mechanical causes, or to over-stimulation. Strychnin sometimes increases, while morphia diminishes, the sense of smell. [**Method of Testing**, § 421.]

344. II. NERVUS OPTICUS.—Anatomical.—The **tractus opticus** (fig. 517, II) arises from the anterior corpora quadrigemina, the corpus geniculatum externum, and the thalamus opticus (fig. 528), as well as from the grey matter which lines the third ventricle (*Tartuferi*). A broad bundle of fibres passes from the origin of the optic tract to the **cortical visual centre**, in the occipital lobe on the same side (*Wernicke*—§ 379, IV.). Fibres pass from the cerebellum through the crura.

The **optic tract** bends round the pedunculus cerebri, where it unites with its fellow of the opposite side to form the **chiasma**, and from the opposite side of this the two **optic nerves** spring.

[**Connections of Optic Tract.**—There is very considerable difficulty in ascertaining the exact origin of all the fibres of the optic tract. Although as yet the statement of Gratiolet is not proved that the optic tract is directly connected with every part of the cerebral hemisphere in man, from the frontal to the occipital lobe, still the researches of D. J. Hamilton have shown that its connections are very extensive. It is certain that some of them are ganglionic, *i.e.*, connected with the ganglia at the base of the brain, while others are *cortical*, and form connections with the cortex cerebri. The **ganglionic** fibres arise from the lateral corpora geniculata, pulvinar, and anterior corpora quadrigemina, and probably also from the substance of the thalamus. The **cortical** fibres join the ganglionic to form the optic tract. According to D. J. Hamilton, the connection with the cortex in the *frontal* region is brought about by "Meynert's commissure." The latter arises directly from the lenticular-nucleus-loop, decussates in the lamina cinerea, and passes into the optic nerve of the opposite side. The lenticular-nucleus-loop is formed below the lenticular nucleus by the junction of the striæ medullares; the striæ medullares form part of the fibres of the internal capsule, and the inner capsule is largely composed of fibres descending from the cortex. Hamilton also asserts that other cortical connections join the tract as it winds round the pedunculus cerebri, and they include (*a*) a large mass of fibres coming from the motor areas of the opposite cerebral hemisphere, crossing in the corpus callosum, entering the outer capsule, and joining the tract directly; (*b*) fibres uniting it to the temporo-sphenoidal lobe of the same side, especially the first and second temporo-sphenoidal convolutions; (*c*) fibres to the gyrus hippocampi of the same side; (*d*) a large leash of fibres forming the "**optic radiation**" of Gratiolet, which connect it directly with the tip of the occipital lobe. There are probably also *indirect* connections with the occipital region through some of the basal ganglia. Although some observers do not admit the connections with the frontal and sphenoidal lobes, all are agreed as to its connection with the occipital by means of the "optic radiation."]

[The **optic radiation** of **Gratiolet** is a wide strand of fibres expanding and terminating in the occipital lobes. It is composed of, or, stated otherwise, gives branches to (*a*) the optic tract directly, (*b*) the corpus geniculatum internum and externum, (*c*) to the pulvinar and substance of the thalamus, (*d*) a direct sensitive band (Meynert's "Sensitive band"), to the posterior third of the posterior limb of the inner capsule, (*e*) fibres which run between the island of Reil and the tip of the occipital lobe (*D. J. Hamilton*).]

Chiasma.—The extent of the decussation of the optic fibres in the chiasma is subject to variations. As a rule, rather more than half of the fibres of one tract cross to the optic nerve of the opposite side (fig. 572), so that the left optic tract sends fibres to the left half of both eyes, while the right tract supplies the right half of both eyes (§ 378, IV.). [Thus, the corresponding regions of each retina are

brought into relation with one hemisphere. The fibres which cross are from the nasal half of each retina (fig. 513).]

Hence, in man, destruction of one optic tract (and its central continuation in the occipital lobe of the cerebrum) produces "**equilateral or homonymous hemianopia.**" In the cat there is a semi-decussation; hence, in this animal extirpation of one eyeball causes atrophy and degeneration of half of the nerve-fibres in both optic tracts (*Gudden*). Baumgarten and Mohr have observed a similar result in man. A sagittal section of the chiasma in the cat produces partial blindness of both eyes (*Nicati*). According to Gudden, the fibres which decussate are

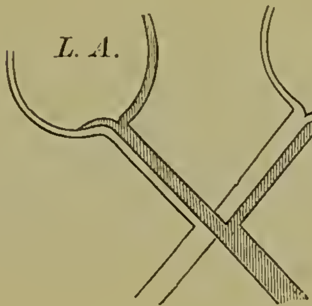


Fig. 512.

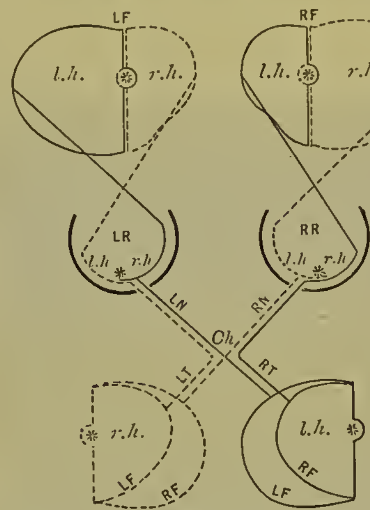


Fig. 513.

Fig. 512.—Scheme of the semi-decussation of the optic nerves. *L.A.*, left eye; *R.A.*, right eye. Fig. 513.—Diagram of the relation of the field of vision, retina, and optic tracts. RF, LF, right and left fields of vision—the asterisk is at the fixing point; RR, LR, right and left retina—the asterisk is at the macula lutea; *l.h.*, *r.h.*, left half and right half of each retina, receiving rays from the opposite half of the field; RN, LN, right and left optic nerves; *Ch*, chiasma; RT, LT, right and left optic tracts; below, the halves of the fields from which impressions pass by each optic tract are superimposed (*Gowers*).

more numerous than those which do not, although J. Stilling maintains that they are only slightly more numerous. According to J. Stilling, the decussating fibres lie in the central axis of the nerve, while those which do not decussate form a layer around the former.

In very rare cases the decussation is absent in man, so that the right tract passes directly into the right eyeball, and the left into the left eyeball (*Vesalius, Caldani*), the sight not being interfered with.

Other observers maintain that there is complete decussation of all the fibres in the chiasma. Hence, *section of one optic nerve* causes dilatation of the pupil and blindness on the *same* side, while section of one *optic tract* causes dilatation of the pupil and blindness of the *opposite* eye (*Knoll*).

Amongst **animals**, there is partial decussation in the rabbit, cat, and dog; total decussation in the mouse, guinea-pig, pigeon, and owl. In osseous fishes, both optic nerves are isolated and merely cross over each other, while in the cyclostomata they do not cross at all. [Total decussation occurs in those animals where the eyes do not act together.]

Injury of the external geniculate body and section of the anterior brachium have the same effect as section of the optic tract of the *same* side (§ 359—*Bechterew*).

It is quite certain that the individual fibres do not divide in the chiasma. Two commissures, the inferior commissure (*Gudden*) and Meynert's commissure, unite both optic tracts further back.

A special commissure (**C. inferior**) extends in a curved form across the posterior angle of the chiasma (*Gudden*). It does not degenerate after enucleation of the eyeballs, so that it is regarded as an intercentral connection. After **excision of an eye**, there is central degeneration of the fibres of the optic nerve entering the eyeball (*Gudden*), and in man about the half of the fibres in the corresponding optic tract (*Baumgarten, Mohr*). After section of **both optic nerves**, or enucleation of both eyeballs, there is a **degeneration**, proceeding centrally, of the whole optic tract. The degeneration extends to the origins in the corpora quadrigemina, external corpora geniculata, and pulvinar, but not into the conducting paths leading to the cortical visual centre (*v. Monakow*) (§ 378, IV. I.). [This shows that perhaps the nerve-cells of the retina are the trophic centres for the fibres of the optic nerve.]

[**Hemianopia** and **Hemianopsia**.—When one optic tract is interfered with or divided, there is interference with or loss of sight in the lateral halves of both retinæ, the blind part being separated from the other half of the field of vision by a vertical line. When it is spoken of as paralysis of one-half of the retina, the term **hemiopia**, or preferably **hemianopia**, is applied to it; when with reference to the field of vision, the term **hemianopsia** is used (see *Eye*). Suppose the *left* optic tract to be divided or pressed upon by a tumour at K (fig. 514), then the outer half of the left and the inner half of the right eye are blind, causing *right lateral hemianopsia, i.e.*, the two halves are affected which correspond in ordinary vision, so that the condition is spoken of as **homonymous hemianopsia**. Suppose the lesion to be at T (fig. 514), then there is paralysis of the *inner* halves of *both* eyes, causing *double temporal hemianopsia*. When there are two lesions at NN, which is very rare, the *outer* halves of both retinæ are paralysed, so that there is *double nasal hemianopsia*. In order to explain some of the eye symptoms that occasionally occur in cerebral disease, Charcot has supposed that some of the fibres which pass from the external geniculate body to the visual centres in the occipital lobe cross behind the corpora quadrigemina, and this is represented in the diagram as occurring at TQ, in the corpora quadrigemina. On this view, all the occipital cortical fibres from one eye would ultimately pass to the cortex of the occipital lobe of the opposite hemisphere. This view, however, by no means explains all the facts, for in cases of homonymous hemianopsia the point of central vision on both sides, *i.e.*, both maculæ luteæ are always unaffected, so that it is assumed that each macula lutea is connected with both hemispheres. The second crossing suggested by Charcot probably does not occur. Affections of the optic nerve, *e.g.*, between the eyeball and the chiasma, *i.e.*, in the orbit, optic foramen, or within the skull, affect one eye only; of the middle of the chiasma, cause temporal hemiopia; of the optic tract, between the chiasma and occipital cortex, hemiopia, which is always symmetrical (*Gowers*).

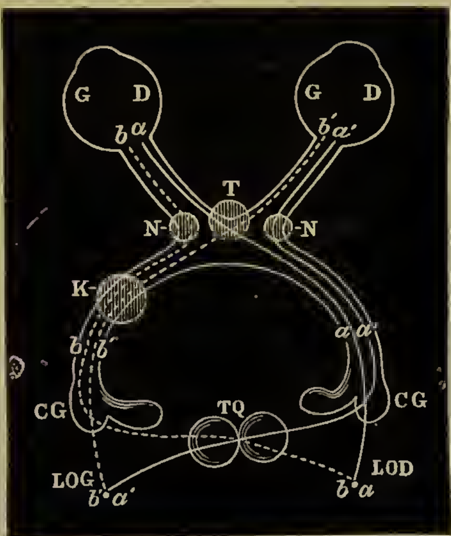


Fig. 514.

Diagram of the decussation of the optic tracts. T, semi-decussation in the chiasma; TQ, decussation of fibres behind the ext. geniculate bodies (CG); $a'b$, fibres which do not decussate in the chiasma; b' a', fibres proceeding from the right eye, and coming together in the left hemisphere (LOG); LOG, K, lesion of the left optic tract producing right lateral hemianopsia; *A*, lesion in the left hemisphere producing crossed amblyopia (right eye); T, lesion producing temporal hemianopsia; NN, lesion producing nasal hemianopsia.

Fig. 513, reduced from that of Gowers, shows the relation of the fields of vision of the retina, tracts, and the cerebral optic centre.

Function. — The optic nerve is the **nerve of sight**; physiologically, it is excited only by the transference of the vibrations of the ether to the rods and cones of the retina (§ 383). Every other form of stimulus, when applied to the nerve in its course or at its centre, causes the sensation of light. Section or degeneration of the nerve is followed by blindness. Stimulation of the optic nerve causes a reflex contraction of the pupils, the efferent nerve being the oculomotorius or third cranial nerve. If the stimulus be very strong, the eyelids are closed and there is a secretion of tears. The influence of light upon the general metabolism is stated at § 126, 9.

As the optic nerve has **special** and independent connections with the (1) so-called *visual centre* (§ 378, IV.), as well as with (2) the *centre for narrowing the pupil* (§ 345), it is evident that, under pathological circumstances, there may be, on the one hand, blindness with retention of the action of the iris, and on the other loss of the movements of the iris, the sense of vision being retained (*Wernicke*).

Gudden found two different kinds of nerve-fibres in the optic nerve; fine or visual fibres, with their centre in the opposite corpora quadrigemina and larger ones—pupil-contracting fibres—arising in the external geniculate body. Destruction of the visual fibres causes blindness, of the others dilatation of the pupil.

Pathological.—Stimulation of almost the whole of the nervous apparatus may cause excessive sensibility of the visual apparatus (**hyperæsthesia optica**), or even visual impressions of the most varied kinds (**photopsia, chromatopsia**), which in cases of stimulation of the visual centre may become actual **visual hallucinations** (§ 378, IV.). Material change in, and inflammation of, the nervous apparatus are often followed by a nervous weakness of vision (**amblyopia**), or even by blindness (**amaurosis**). Both conditions, however, may be the signs of disturbances of other organs, *i.e.*, they are "sympathetic" signs, due it may be to changes in the movement of the blood-stream, depending upon stimulation of the vaso-motor nerves. The discovery of the partial origin of the optic nerve from the spinal cord explains the occurrence of ambylopia with partial atrophy of the optic nerve, in disease of the spinal cord, especially in tabes. Many **poisons**, such as lead and alcohol, disturb vision. There are remarkable intermittent forms of amaurosis known as day-blindness or **hemeralopia**, which occurs in some diseases of the liver, and is sometimes associated with incipient cataract. [The person can see better in a dim light than during the day or in a bright light. In night-blindness or **nyctalopia**, the person cannot see at night or in a dim light, while vision is good during the day or in a bright light. It depends upon disorder of the eye itself, and is usually associated with imperfect conditions of nutrition.]

345. **III. NERVUS OCULOMOTORIUS.**—**Anatomical.**—It springs from the **oculomotorius nucleus** (united with that of the trochlearis), which is a direct continuation of the anterior horn of the spinal cord, and lies under the aqueduct of Sylvius (figs. 517, 520). [The motor nucleus (fig. 516) gives origin to three sets of fibres, for (1) the most of the muscles of the eye-balls, (2) the sphincter pupillæ, (3) ciliary muscle. The nucleus of the 3rd and 4th nerves is also connected with that of the 6th under the iter, so that all the nerves to the ocular muscles are thus co-related at their centres.]

The origin is connected with the corpora quadrigemina, to which the intraocular fibres may be traced, and also with the opposite half of the brain to the angular gyrus (§ 378, I.) through the pedunculus cerebri. Beyond the pons, it appears on the inner side of the cerebral peduncle, between the superior cerebellar and posterior cerebral arteries (fig. 517, III).

Functions.—It contains—(1) the voluntary motor fibres for all the external muscles of the eyeballs—except the external rectus and superior oblique—and for the levator palpebræ superioris. The co-ordination of the movements of both eyeballs, however, is independent of the will. (2) The fibres for the **sphincter pupillæ**, which are excited reflexly from the retina. (3) The voluntary fibres for the **muscle of accommodation**, the tensor choroideæ or ciliary muscle. The intrabulbar fibres of 2 and 3 proceed from the branch for the inferior oblique muscle, as the short root of the ciliary ganglion (fig. 518). They reach the eyeball through the short ciliary nerves of the ganglion. V. Trautvetter and others observed that stimulation of the nerve caused changes in the eye similar to those which accompany near vision. The three centres for the muscle of accommodation, the sphincter pupillæ, and the internal rectus muscle, lie directly in relation with each other, in the most posterior part of the floor of the third ventricle (*Hensen and Völckers*).

The **centre** for the *reflex* stimulation of the sphincter fibres by light was said to be in the corpora quadrigemina, but newer researches locate it in the medulla oblongata (§§ 379, 392). The narrowing of the pupil, which accompanies the act of accommodation for a near object, is to be regarded as an associated movement (§ 392, 5).

Anastomoses.—In man, the nerve anastomoses on the sinus cavernosus with the ophthalmic branch of the trigeminus, whereby it receives *sensory fibres for the muscles* to which it is distributed (*Valentin, Adamük*), with the sympathetic through the carotid plexus, and (?) indirectly through the abducens, whereby it receives vaso-motor fibres (?).

Varieties.—In some rare cases, the pupillary fibres for the sphincter run in the abducens (*Adamük*), or even in the trigeminus (*Schiff, v. Gräfe*).

Atropin paralyses the intrabulbar fibres of the oculomotorius, while **Calabar bean** stimulates them (or paralyses the sympathetic, or both—compare § 392).

Stimulation of the nerve, which causes contraction of the pupil, is best demonstrated on the decapitated and opened head of a bird. The pupil is dilated in paralysis of the oculomotorius, in asphyxia, sudden cerebral anæmia (*e.g.*, by ligature of the carotids, or beheading), sudden venous congestion, and at death.

Pathological.—Complete paralysis of the oculomotorius is followed by—(1) drooping of the upper eyelid (**ptosis paralytica**); (2) immobility of the eyeball; (3) squinting (strabismus) out-

wards and downwards, and consequently there is double vision (**diplopia**); (4) slight protrusion of the eyeball, because the action of the superior oblique muscle in pulling the eyeball forward is no longer compensated by the action of three paralysed recti muscles. In animals provided with a retractor bulbi muscle, the protrusion of the eyeball is more pronounced; (5) moderate dilatation of the pupil (**mydriasis paralytica**); (6) the pupil does not contract to light; (7) inability to accommodate for a near object. It is to be noted, however, that the paralysis may be confined to individual branches of the nerve, *i.e.*, there may be incomplete paralysis.

[**Squinting.**—In **paralysis** of the **superior rectus**, the eye cannot be moved upwards, and specially upwards and outwards. There is diplopia on looking upwards, the false image being above the true, and turned to the right when the left eye is affected (fig. 515, 3). **Inferior Rectus.**—Defect of downward, and especially downward and outward movement, the eye being directed upwards and outwards. Diplopia with crossed images, the false one is below the true image and placed obliquely, being turned to the left when the left eye is affected. Diplopia is

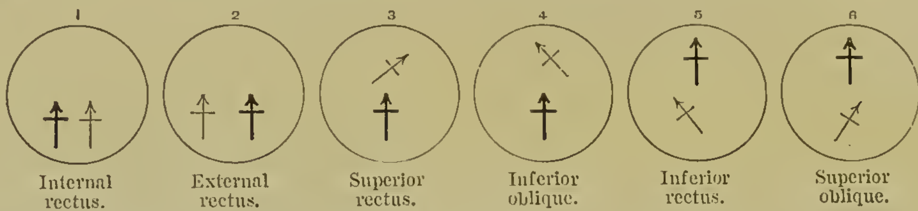


Fig. 515.

The black cross represents the true image, the thin cross the false image. The left eye is represented as affected in all cases (*Bristow*).

most troublesome when the object is below the line of vision (fig. 515, 5). **Internal Rectus.**—Defective inward movement, divergent squint, and diplopia, the images being on the same plane, the false one to the patient's right when the left eye is affected. The head is turned to the healthy side, when looking at an object, while there is secondary deviation of the healthy eye outwards (fig. 515, 1). **Inferior oblique**—is rare, the eye is turned slightly downwards and inwards, and defective movement upwards. Diplopia with the false image above the true one, especially on looking upwards; the false image is oblique, and directed to the patient's left when the left eye is affected (fig. 515, 4).]

Stimulation of the branch supplying the levator palpebræ in man causes **lagophthalmus spasticus**, while stimulation of the other motor fibres causes a corresponding **strabismus spasticus**. The latter form of squinting may be caused also reflexly—*e.g.*, in teething, or in cases of diarrhœa in children; [the presence of worms or other source of irritation in the intestines of children is a frequent cause of squinting]. Clonic spasms occur in *both* eyes, and also as involuntary movements of the eyeballs constituting **nystagmus**, which may be produced by stimulation of the corpora quadrigemina, as well as by other means. Tonic contraction of the sphincter pupillæ is called **myosis spastica**, and clonic contraction, **hippus**. Spasm of the muscle of accommodation (ciliary muscle) is sometimes observed; owing to the imperfect judgment of distance, this condition is not unfrequently associated with macropia.

[**Conjugate Deviation.**—Some movements are produced by non-corresponding muscles; thus, on looking to the right, we use the right external rectus and left internal rectus, and the same is the case in turning the head to the right, *e.g.*, the inferior oblique, some muscles of the right side act along with the left sterno-mastoid. In hemiplegia, the muscles on one side are paralysed, so that the head and often the eyes are turned away from the paralysed side, *i.e.*, to the side of the brain on which the lesion occurs. This is called "**conjugate deviation**" of the eyes, with rotation of the head and neck. If the right external rectus be paralysed from an affection of the sixth nerve, on telling the patient to look to the right it will be found that the left eye will squint more inwards even than the right eye, *i.e.*, owing to the strong voluntary effort, the muscle, the left internal rectus, which usually acts along with the right external rectus, contracts vigorously, and so we get **secondary deviation** of **the sound eye**. Similar results occur in connection with paralysis of other ocular muscles.]

346. **IV. NERVUS TROCHLEARIS.—Anatomical.**—It arises from the valve of Vieussens, *i.e.*, *behind* the fourth ventricle, but its fibres pass to the oculomotorius from the *trochlearis nucleus*, which is to a certain extent a continuation of the anterior horn of the spinal cord (figs. 516, 520). It passes to the lower margin of the corpora quadrigemina, pierces the roof of the aqueduct of Sylvius, then into the velum medullare superius, and after **decussating** with the root of the opposite side behind the iter, it pierces the crus at the superior and external border (fig. 517). Its fibres cross between its nucleus and its distribution. It has also an origin from the locus cœruleus. The root of the nerve receives some fibres from the nucleus of the abducens of the opposite side. Physiologically, there is a necessity for a connection between the centre and the cortical motor centre for the eye muscles.

Function.—It is the voluntary motor nerve of the superior oblique muscle. (In co-ordinated movements, however, it is involuntary.)

Anastomoses.—Its connections with the plexus carotidus sympathici, and with the first branch of the trigeminus, have the same significance as similar branches of the oculomotorius.

Pathological.—Paralysis of the trochlearis nerve causes a very slight loss of the mobility of the eyeball outwards and downwards. There is slight squinting inwards and upwards, with

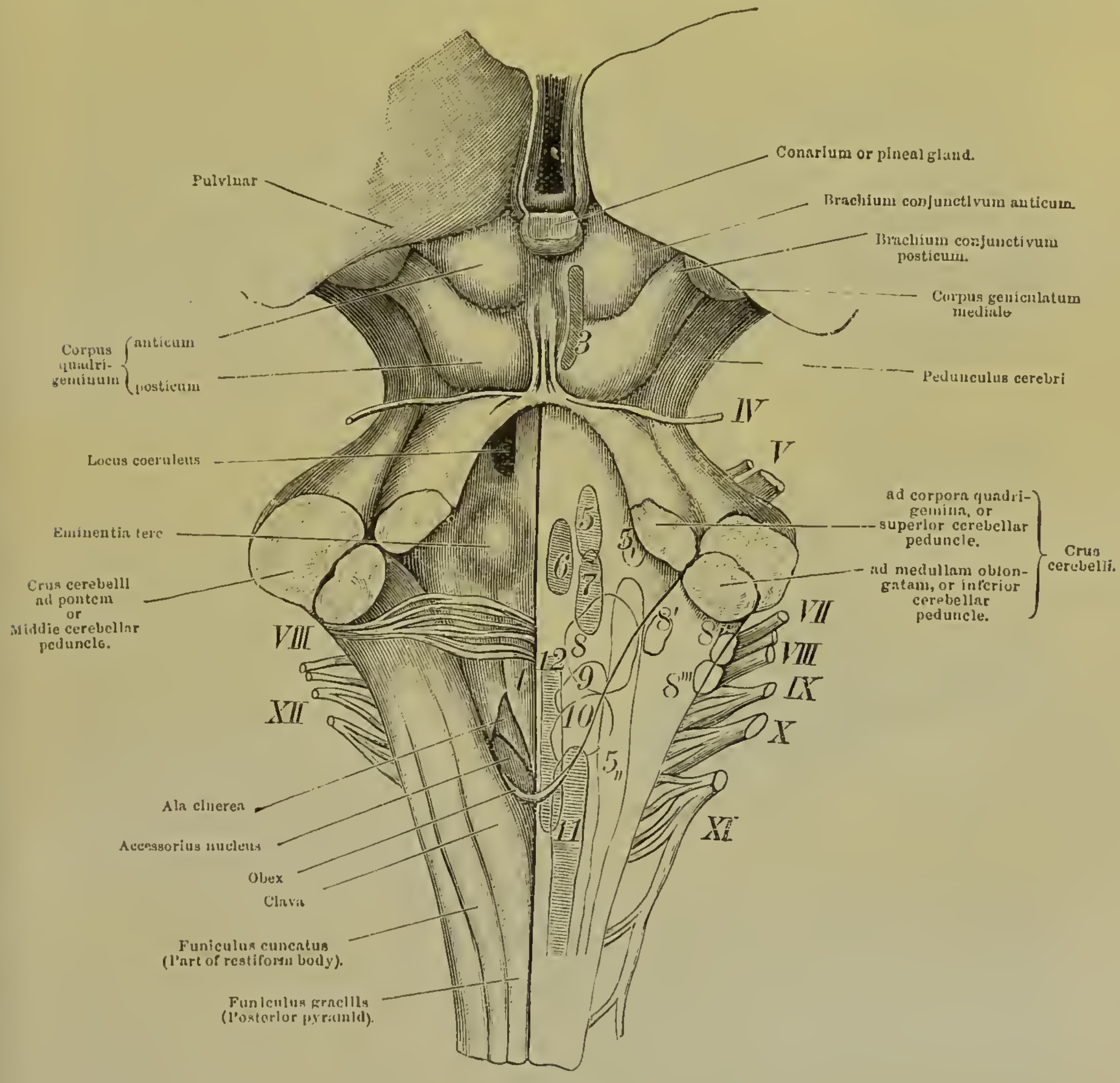


Fig. 516.

Medulla oblongata, with the corpora quadrigemina. The numbers *IV–XII* indicate the superficial origins of the cranial nerves, while these (3–12) indicate their deep origin, *i.e.*, the position of their central nuclei ; *t*, funiculus teres.

diplopia or double vision. The images are placed obliquely over each other [the false image being the lower, and directed to the patient's right when the left eye is affected (fig. 515, 6)] ; they approach each other when the head is turned towards the sound side, and are separated when the head is turned towards the other side. The patient at first directs his head forwards, later he rotates it round a vertical axis towards the sound side. In rotating his head (whereby the *sound* eye may retain the primary position), the eye rotates with it. Spasm of the trochlearis causes squinting outwards and downwards.

347. V. NERVUS TRIGEMINUS.—**Anatomical.**—The trigeminus (fig. 518, 5) arises like a spinal nerve by two roots (fig. 517, V.) The smaller, anterior, motor root proceeds from

the "motor trigeminal nucleus" (5), which is provided with many multipolar nerve-cells, and lies in the floor of the medulla oblongata, not far from the middle line (fig. 520). Fibres connect this nucleus with the cortical motor centres on the opposite side of the cerebrum. Besides this the "descending root" also supplies motor fibres. It extends laterally from the corpora quadrigemina along the aqueduct of Sylvius downwards to the exit of the nerve (*Henle*, *Forel*). The large posterior sensory root receives fibres :—(1) From the small cells of the "sensory trigeminal nucleus" which lies at the level of the pons, and is the analogue of the posterior horn of the grey matter of the spinal cord. (2) From the grey matter of the posterior horn of the spinal cord, downwards as far as the second cervical vertebra. These fibres run into the posterior column of the cord and then appear as the "ascending root" in the trigeminus. (3) Some fibres come from the cerebellum, through the crura cerebelli. The origins of the sensory root anastomose with the motor nuclei of all the nerves arising from the medulla oblongata, with the exception of the abducens. This explains the vast number of reflex relations of the fifth nerve. The thick trunk appears on each side of the pons (fig. 517), when its posterior root (perhaps in connection with some fibres from the anterior) forms the Gasserian ganglion, upon the tip of the petrous part of the temporal bone (fig. 518). Fibres from the sympathetic proceed from the plexus cavernosus to the ganglion. The nerve divides into three large branches.

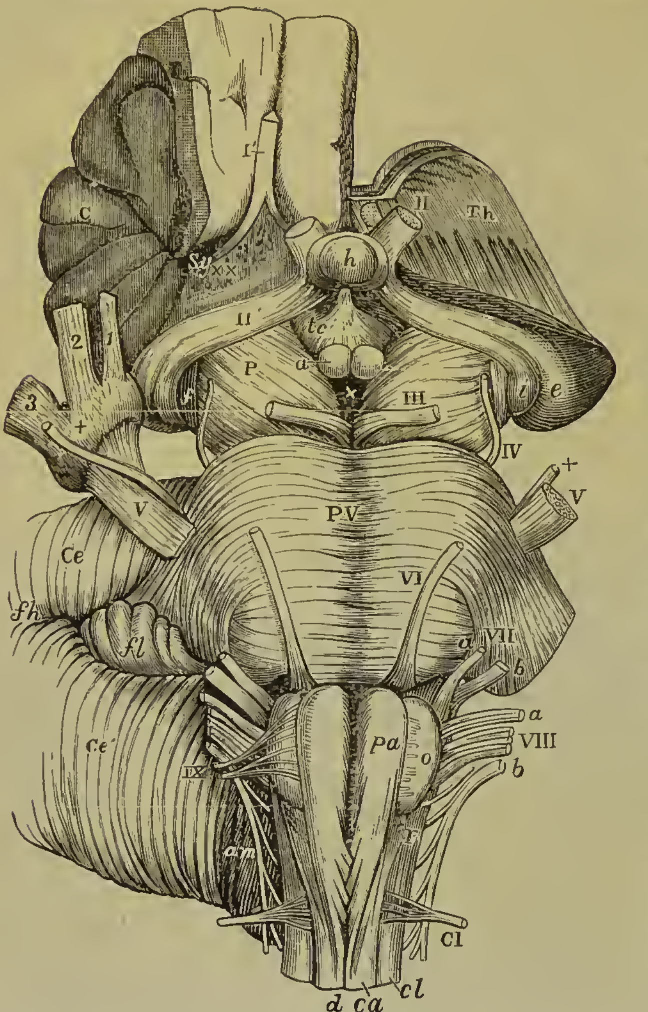


Fig. 517.

Part of the base of the brain, with the origins of the cranial nerves ; the convolutions of the island of Reil on the right side, but removed on the left. I′, olfactory tract cut short ; II, left optic nerve ; II′, right optic tract ; *Th*, cut surface of the optic left thalamus ; C, central lobe, or island of Reil ; *Sy*, fissure of Sylvius ; XX, the locus perforatus anticus ; *e*, the external, and *i*, the internal corpus geniculatum ; *h*, hypophysis cerebri ; *tc*, tuber cinereum, with the infundibulum ; *a*, points to one of the corpora albicantia; P, the cerebral peduncle ; *f*, the fillet ; III, left oculomotor nerve ; X, the locus perforatus posticus ; PV, pons Varolii ; V, the greater part of the fifth nerve ; +, the lesser root (on the right side this mark is placed on the Gasserian ganglion and points to the lesser root) ; 1, ophthalmic division of the fifth ; VII *a*, facial, VII *b*, auditory ; VIII, vagus ; VIII *a*, glosso-pharyngeal ; VIII *b*, spinal accessory ; IX, hypoglossal ; *fl*, flocculus ; *fh*, horizontal fissure of the cerebellum (*Ce*) ; *am*, amygdala ; *pa*, anterior pyramid ; *o*, olivary body ; *c*, restiform body ; *d*, anterior median fissure ; *cl*, the lateral column of the spinal cord ; Cl, the sub-occipital or first cervical nerve.

I. The ophthalmic division (fig. 518, *d*) receives *sympathetic* fibres (*vaso-motor nerves*) from the plexus cavernosus ; it passes through the superior orbital fissure [sphenoidal] into the orbit. Its branches are :—

1. The small recurrent nerve which gives sensory branches to the tentorium cerebelli. Fibres — the vaso-motor nerves for the dura mater—proceed along with it from the carotid plexus of the sympathetic.

2. The lachrymal nerve gives off—(*a*) Sensory branches to the conjunctiva, the upper eyelid, and the

neighbouring part of the skin over the temple (fig. 518, *a*); (*b*) true **sensory** fibres to the lachrymal gland (?). Stimulation of this nerve is said to cause a secretion of tears, while its section prevents the reflex secretion excited through the sensory nerves of the eye. After a time, section of the nerve is followed by a paralytic secretion of tears (*Herzenstein and Wolferz*), although the statement is contested by Reich. The secretion of tears may be excited reflexly, by strong stimulation of the retina by light, by stimulation of the first and second branches of the trigeminus, and through all the sensory cranial nerves (*Demtschenko*) (§ 356, A, 6).

3. The **frontal** (*f*) gives off the **supratrochlear**, which supplies **sensory** fibres to the upper eyelids, brow, glabella, and those which excite the **secretion of tears** reflexly; and by its **supraorbital** branch (*b*), analogous branches to the upper eyelid, skin of the forehead, and the adjoining skin over the temple as far as the vertex.

4. The **naso-ciliary** nerve (*nc*), by its **infratrochlear** branch supplies fibres, similar to those of 3, to the conjunctiva, caruncula, and saccus lacrimalis, the upper eyelid, brow, and root of the nose. Its **ethmoidal** branch supplies the tip and alæ of the nose, outside and inside, with sensory branches, as well as the upper part of the septum and the turbinated bones with **sensory** fibres, which can act as afferent nerves in the reflex secretion of tears; while it is probable that **vaso-motor** fibres are supplied to these parts through the same channel. (These fibres may be derived from the anastomosis with the sympathetic (?).) The naso-ciliary nerve gives off the long root (*l*) of the ciliary ganglion (*c*), and 1 to 3 long ciliary nerves.

The **ciliary ganglion** (fig. 518, *c*), which, according to Schwalbe, perhaps belongs rather to the third than the fifth nerve, has **three roots**—(*a*) the **short** or oculomotorius (3—see § 345); (*b*) the **long** (*l*), from the naso-ciliary; and (*c*) the **sympathetic** (*s*) sometimes united with *b*, from the carotid plexus. The **short ciliary nerves** (*t*), six to ten in number, proceed from the ganglion, along with the long ciliary nerves, to near the entrance of the optic nerve, where they perforate the sclerotic coat and run forwards between it and the choroid.

Ciliary Nerves.—*Physiologically*, these nerves contain :—

1. The **motor fibres** for the **sphincter pupillæ** and the **tensor choroideæ** from the root of the oculomotorius (§ 345, 2, 3).

2. **Sensory** fibres for the **cornea**, which are distributed as excessively fine fibrils between the epithelium of the *conjunctiva bulbi*; they perforate the sclerotic. These fibres cause a reflex secretion of tears (N. lacrimalis) and closure of the eyelids (N. facialis). Sensory fibres are supplied to the **iris** (pain in iritis and in operations on the iris), the **choroid** (painful tension when the ciliary muscle is strained), and the **sclerotic.**

3. **Vaso-motor nerves** for the blood-vessels of the iris, choroid, and retina. They arise in part from the **sympathetic** root, and the anastomosis of the sympathetic with the ophthalmic division of the trigeminus (*Wegner*). The **iris** and **retina** receive most of their vaso-motor nerves from the trigeminus itself (*Rogow*), and few from the sympathetic; according to Klein and Svetlin, the retinal vessels are not influenced either by stimulation or division of the sympathetic.

4. **Motor fibres** for the **dilator pupillæ**, which for the most part are derived from the *sympathetic* (*Petit*, 1727), through the sympathetic root of the ganglion and the anastomosis of the sympathetic with the trigeminus (*Balogh*, *Oehl*). Some observers deny altogether the existence of a dilator pupillæ muscle (§ 384). The ophthalmic division contains independent fibres for the dilatation of the pupil (*Schiff*), which arise in the medulla oblongata and proceed directly into the ophthalmic (? or arise from the Gasserian ganglion—*Oehl*).

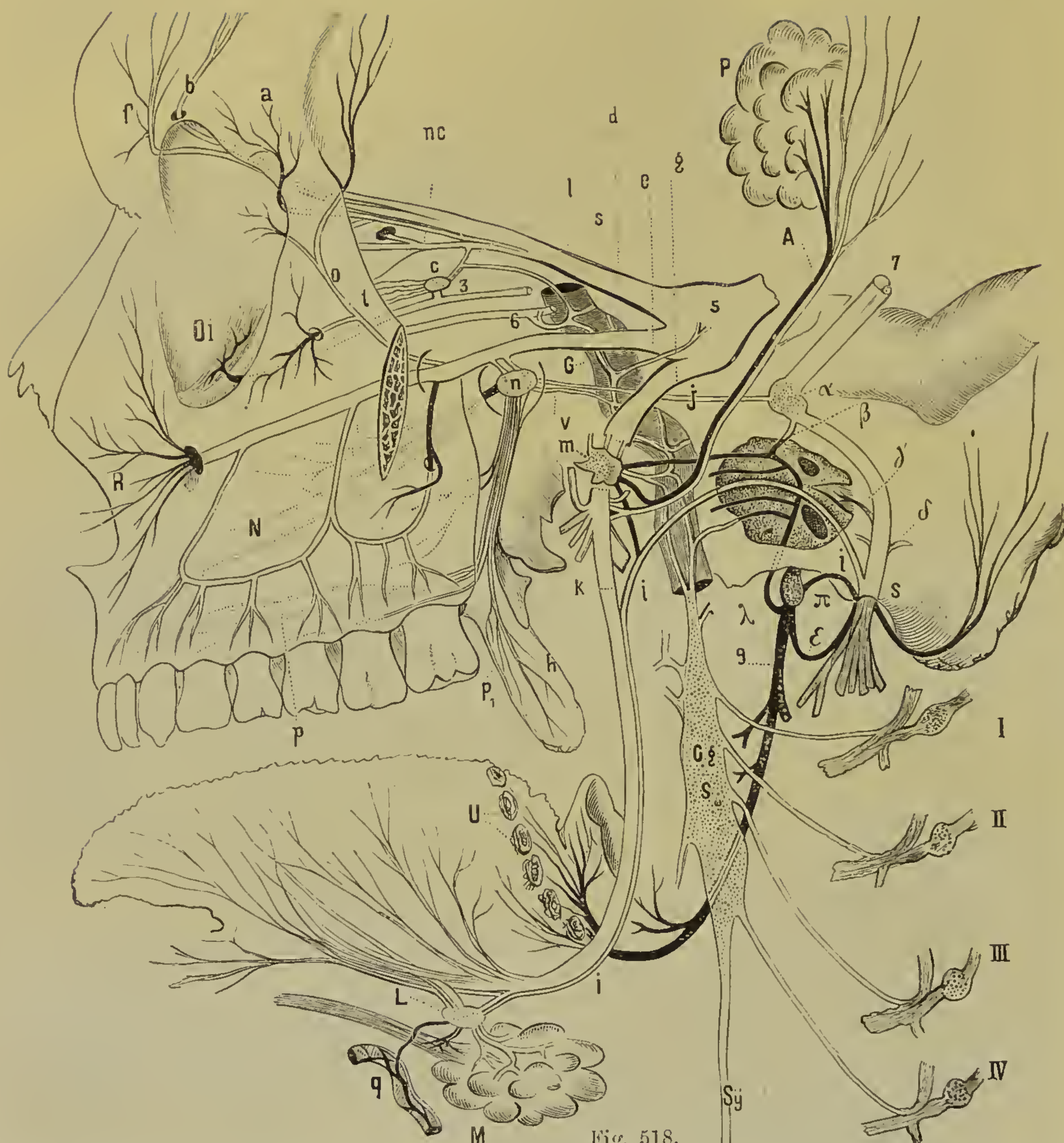


Fig. 518.

Semi-diagrammatic representation of the nerves of the eyeball, the connections of the trigeminus and its ganglia, together with the facial and glosso-pharyngeal nerves. 3. Branch to the inferior oblique muscle from the oculomotorius, with the thick short root, to the ciliary ganglion (*c*); *t*, ciliary nerves; *l*, long root to the ganglion from the naso-ciliary (*nc*); *s* sympathetic root from the sympathetic plexus (*Sy*) surrounding the internal carotid (G); *d*, first or ophthalmic division of the trigeminus (5), with the naso-ciliary (*nc*), and the terminal branches of the lachrymal (*a*), supra-orbital (*b*), and frontal (*f*); *e*, second or superior maxillary division of the trigeminus; R, infra-orbital; *n*, spheno-palatine (Meckel's) ganglion with its roots; *j*, from the facial, and *v*, from the sympathetic; N, the nasal branches, and pp_1, the palatine branches of the ganglion; *g*, third or inferior maxillary division of the trigeminus; *k*, lingual; *i i*, chorda tympani; *m*, otic ganglion, with the roots from the tympanic plexus, the carotid plexus, and from the 3rd branch, and with its branches to the auriculo-temporal (A), and to the chorda (*i i*); L, sub-maxillary ganglion with its roots from the tympanico-lingual, and the sympathetic plexus on the external artery (*q*). 7. Facial nerve—*j*, its great superficial petrosal branch; α, gang. geniculatum; β, branch to the tympanic plexus; γ, branch to the stapedius; δ, anastomatic twig to the auricular branch of the vagus; *i i*, chorda tympani; S, stylo-mastoid foramen. 9. Glosso-pharyngeal—λ, its tympanic branch; π and ε, connections with the facial: U, terminations of the gustatory fibres of 9 in the circumvallate papillæ; *Sy*, sympathetic with *G g*, *s*, the superior cervical ganglion; *I*, *II*, *III*, *IV*, the four upper cervical nerves; P, parotid, M, sub-maxillary gland.

It is not conclusively determined whether in man dilator fibres also proceed through the sympathetic root of the ciliary ganglion, and reach the iris through the ciliary nerves. In the dog and cat these fibres do not pass through the ciliary ganglion, but go directly along the optic nerve to the eye (*Hensen and Völckers*) through the Gasserian ganglion, to its ophthalmic branch and through the long ciliary nerves (*Jegorow*). In birds, the dilator fibres run only in the fifth (*Zeglinski*). For the centre (§ 367, 8).

After **section of the trigeminus** the pupil becomes contracted after a short period of dilatation (rabbit, frog), but this effect is not permanent. After excision of the superior cervical ganglion of the sympathetic, the power of dilatation of the pupil is not completely abolished. The narrowing of the pupil which follows section of the trigeminus in the rabbit, and which rarely lasts more than half an hour, may be regarded as due to a reflex stimulation of the oculomotorius fibres of the sphincter, in consequence of the painful stimulation caused by section of the trigeminus.

Stimulation of the Cervical Sympathetic.—Either in the neck, or in its course to the eye, when the peripheral end of the cervical sympathetic is stimulated, besides causing constriction on the blood-vessels on that side of the head, there is *dilatation of the pupil*, as well as contraction of the *smooth muscular fibres* in the orbit and eyelids. The membrana orbitalis, which separates the orbit from the temporal fossa in animals, contains numerous smooth muscular fibres (*muscular orbitalis*). The corresponding membrane of the inferior orbital fissure [spheno-maxillary fissure] in man has a layer of smooth muscle, one millimetre thick, and arranged for the most part longitudinally. Both *eyelids* contain smooth muscular fibres which serve to close them ; in the upper lid they lie as if they were a continuation of the levator palpebræ superioris, in the lower lid they lie close under the conjunctiva. *Tenon's capsule* also contains smooth muscular fibres. The sympathetic nerve supplies all these muscles (*Heinr. Müller*)—(the orbital muscle is partly supplied from the spheno-palatine ganglion) ; in animals, the retractor of the third eyelid at the inner angle of the eye is similarly supplied. Hence, *stimulation of the sympathetic* causes dilatation of the pupil and of the palpebral fissure, with protrusion of the eyeball. This result may be caused reflexly by strong stimulation of sensory nerves. Strong stimulation of the nerves of the sexual organs is followed by similar phenomena in the eye. The dilatation of the pupil, which occurs in children affected with intestinal worms, is perhaps an analogous phenomenon. The pupil is dilated when the spinal cord is stimulated (at the origin of the sympathetic), as in tetanus.

Section of the cervical sympathetic, besides other effects, notably those on the blood-vessels on that side of the head and face (fig. 532), causes narrowing of the fissure between the eyelids, the eyeball sinks in its socket (and in animals, the third eyelid is relaxed and protruded). In dogs, section causes internal squint, as the external rectus receives some motor fibres from the sympathetic. (Origin of these fibres from the cilio-spinal region. *Spinal Cord*, § 362, 1.)

5. It is probable that **trophic fibres** occur in the trigeminus, and pass through the ciliary nerves to reach the eye. If the trigeminus be divided within the cranium, after six to eight days, inflammation, necrosis of the cornea, and ultimately complete destruction of the eyeball take place, constituting **panophthalmia** (*Fodèra*, 1823 ; *Magendie*).

Trophic Fibres in the fifth nerve.—In weighing the evidence for and against the existence of trophic fibres, we must bear in mind the following considerations :—1. **Section of the trigeminus** makes the whole **eye insensible** ; the animal is therefore unconscious of direct injury to its eye, and cannot therefore remove any offending body. Dust or mucus, which may adhere to the eye, is no longer removed by the reflex closing of the eyelids ; while, owing to the absence of the reflex, the eye is more open and is therefore subject to more injuries ; the reflex secretion of tears is also arrested. Snellen (1857) fixed the ear of a rabbit in front of its eye so as to protect the latter and shield it from injuries, and he found that the inflammation and other events occurred at a later date, while, according to Meissner and Büttner, if the eye be protected by means of a complete capsule, the inflammation does not occur at all. There can be no doubt that the loss of the sensibility of the eye favours the occurrence of inflammation. But Meissner, Büttner, and Schiff observed that inflammation of the eye occurred when the **trophic** (most internal) fibres alone were divided, the eye at the same time retaining its sensibility ; this would seem to indicate the existence of trophic fibres, but Cohnheim and Senftleben dispute the statement. Conversely, the sensibility of the eye may be abolished by partial section of the nerve, yet the eye does not become inflamed (*Schiff*). Ranvier, who denies the existence of trophic nerves, made a circular incision round the margin of the cornea through its superficial layers, so as to divide all the corneal nerves. Insensibility of the cornea was thereby produced, but never keratitis. Further, in man and animals, when they are unable to close their eyelids, there is redness with secretion

of tears, or slight dryness and opacity of the surface of the eyeball (**xerosis**), but never the inflammation already described (*Samuel*). 2. We must also take into consideration the following:—Section of the trigeminus paralyses the vaso-motor nerves in the interior of the eyeball, which must undoubtedly cause a disturbance in the intraocular circulation. According to Jesner and Grünhagen, the trigeminus also contains *vaso-dilator fibres*, whose stimulation is followed by increased flow of blood to the eye, with consecutive excretion of the fibrin-factors and increase in the amount of albumin of the aqueous humour. 3. After section of the nerve, the **intraocular tension is diminished** (while stimulation of the nerve is followed by increase of the intraocular pressure (*Hippell, Grünhagen*). This diminution of the normal tension necessarily must alter the normal relation of the filling of the blood- and lymph-vessels, and also the movement of the fluids, upon which the normal nutrition is largely dependent. 4. Kühne observed that stimulation of the corneal nerves was followed by contraction of the so-called corneal corpuscles. Perhaps the movements of these corpuscles may influence the normal movement of the lymph in the canalicular system of the cornea (§ 384); these movements, however, would seem to depend upon the nervous system, so that its destruction is likely to produce disturbance of nutrition.

[There are **three conditions** on which the changes may depend—(1) mere loss of sensibility, which alone is not sufficient to explain the phenomena; (2) vaso-motor disturbance, which is excluded by the above facts, and also by the other consideration that, if the fifth nerve be divided and the superior cervical ganglion excised simultaneously, ophthalmia does not occur, and, in fact, excision of this sympathetic ganglion may modify the results of section of the fifth (*Sinitzin*). Thus, we are forced to (3) the theory of trophic fibres, whose centre is the Gasserian ganglion.]

Pathological.—In cases of anæsthesia of the trigeminus in man, and, more rarely, in severe irritation of this nerve, inflammation of the conjunctiva, ulceration and perforation of the cornea, and finally panophthalmia, have been observed (*Charles Bell*). This condition has been called **ophthalmia neuroparalytica.** Samuel found that a similar result was produced by electrical stimulation of the Gasserian ganglion in animals.

There are other affections of the eye depending upon disease of the **vaso-motor nerves**, which are quite different from the foregoing, as they never lead to degenerative changes. Such is **ophthalmia intermittens** (due to malaria), a unilateral, intermittent, excessive filling of the blood-vessels of the eye, accompanied by the secretion of tears, photophobia, often accompanied by iritis and effusion of pus into the chambers of the eye. This condition is regarded by Eulenburg as a vasoneurotic affection of the ocular blood-vessels. Pathological observations, as well as experiments upon animals, have shown that there is an intimate physiological connection between the vascular areas of both eyes, so that affections of the vascular area of one eye are apt to induce similar disturbances of the opposite eye. This serves to explain the fact that inflammatory processes in the interior of one eyeball are apt to produce a similar condition in the other eye. This is the so-called "**sympathetic ophthalmia.**" Thus, stimulation of the ciliary nerves, or the fifth on *one* side, causes dilatation of the blood-vessels not only on its own side but also on the other side as well (*Jesner and Grünhagen*). The pathological condition of **glaucoma simplex**, where the intraocular tension is greatly increased, is ascribed by Donders to irritation of the trigeminus. [Increased intraocular tension may be produced by irritation of the secretory fibres contained in the fifth nerve (*Donders*), by stimulating the nucleus of the trigeminus in the medulla oblongata (*Hippell and Grünhagen*), and also reflexly by irritation of the peripheral branches of the fifth, as by nicotin placed in the eye. It is possible, however, that some forms of glaucoma are produced by diminished removal of the aqueous humour from the eye.] Unilateral secretion of tears, due to irritation of the ophthalmic division of the fifth, has been repeatedly observed, but unilateral cessation of tears, due to paralytic conditions, very rarely.

II. Superior Maxillary Division (fig. 518, *e*).—It gives off—

1. The delicate **recurrent nerve**, a **sensory** branch to the dura mater, which accompanies the **vaso-motor** nerves, derived from the superior cervical ganglion of the sympathetic, and is distributed to the area of the middle meningeal artery.

2. The **subcutaneous malar** or orbital (*o*) supplies by its temporal and orbital branches **sensibility** to the lateral angle of the eye and the adjoining area of skin of the temple and cheek. Certain fibres are said to be the true secretory nerves for tears. Compare N. lacrimalis, p. 724.

3. The **dental**, anterior, posterior, and median, and with them the anterior fibres from the infraorbital nerve, supply **sensory** fibres to the teeth in the upper jaw, the gum, periosteum, and the cavities of the jaw (p. 726). The vaso-motor nerves of all these parts are supplied from the upper cervical ganglion of the sympathetic.

4. The **infraorbital** (R), after its exit from the infraorbital foramen, supplies

sensory nerves to the lower eyelid, the bridge and sides of the nose, and the upper lip as far as the angle of the mouth. The accompanying artery receives its vaso-motor fibres from the superior cervical ganglion of the sympathetic. For the **sweat-secreting** fibres which occur in it (pig) see § 288.

The **spheno-palatine ganglion (Meckel's**—n) forms connections with the second division. To it pass two short **sensory** root-fibres from the second division itself, which are called *spheno-palatine.* **Motor** fibres enter the ganglion from behind, through the large superficial petrosal branch of the facial (j); and grey **vaso-motor** fibres (v) from the sympathetic plexus on the carotid (the deep large petrosal nerve). The motor and vaso-motor fibres from the Vidian nerve, which reach the ganglion through the canal of the same name.

Branches of Meckel's Ganglion.—(1) The **sensory fibres** (N) which supply the roof, lateral walls, and septum of the nose (posterior and superior nasal); the terminal fibres of the *naso-palatine* pass through the canalis incisivus to the hard palate, behind the incisor teeth. The sensory inferior and posterior nasals for the lower and middle turbinated bones, and both lower nasal ducts, are derived from the *anterior* palatine branch of the ganglion, which descends in the palato-maxillary canal. Lastly, the sensory branches for the hard (p) and soft palate (p_1), and the tonsils arise from the *posterior* palatine nerve. All the sensory fibres of the nose (see also the *Ethmoidal nerve*), when stimulated, cause the reflex act of **sneezing** (§ 120). Preparatory to the act of sneezing, there is always a peculiar feeling of tickling in the nose, which is perhaps due to dilatation of the nasal blood-vessels. This dilatation is rapidly caused by cold, more especially when it is applied directly to the skin. The dilatation of the vessels is followed by an increased secretion of watery fluid from the nasal mucous membrane. Stimulation of the nasal nerves also causes a reflex secretion of **tears**, and it may also cause stand-still of the respiratory movements in the expiratory phase (*Hering and Kratschmer*)—(compare *Respiratory centre*, § 368). (2) The **motor branches** descend in the posterior palatine nerve through the small palatine canal, and give off (h) motor branches to the elevator of the soft palate and azygos uvulæ (*Nuhn*). [Beevor and Horsley find that in the monkey the levator palati is not supplied from the facial nerve *viâ* the superficial petrosal nerve, for stimulation of the seventh nerve at its origin does not cause any movement in the palate. They suggest that this muscle is supplied by the spinal accessory nerve, perhaps through the upper branches of the pharyngeal plexus.] The sensory fibres for these muscles are supplied by the trigeminus. According to Politzer, spasmodic contraction of these muscles occasionally causes crackling noises in the ears. (3) The **vaso-motor** nerves of this entire area arise from the sympathetic root, *i.e.*, from the upper cervical ganglion. (4) The root of the trigeminus supplies the **secretory nerves** of the mucous glands of the nasal mucous membrane. Stimulation excites secretion, while section of the trigeminus diminishes it with simultaneous atrophic degeneration of the mucous membrane. Thus, **trophic** functions for the mucosa have been ascribed to the trigeminus (*Aschenbrandt*).

Stimulation of the Ganglion.—Feeble electrical stimulation of the exposed ganglion causes a copious secretion of mucus and an increase of the temperature in the nose (*Prévost*), with dilation of the vessels (*Aschenbrandt*). [Meckel's ganglion has been excised in certain cases of neuralgia (*Walsham*).]

III. Inferior Maxillary (g).—It contains all the **motor fibres** of the fifth, along with a number of **sensory** fibres; it gives off—

1. The **recurrent**, which springs by itself from the *sensory* root, enters the skull through the foramen spinosum, and, along with the nerve of the same name from the II. division, supplies **sensory** fibres to the dura mater. Fibres proceed from it through the petroso-squamosal fissure to the mucous membrane of the cells of the mastoid process.

2. **Motor** fibres for the **muscles of mastication**, viz., the masseteric, the two deep temporal nerves, and the internal and external pterygoid nerves. The sensory fibres for the muscles are supplied by the sensory fibres.

3. The **buccinator** is a *sensory* nerve for the mucous membrane of the cheek, and the angle of the mouth as far as the lips.

According to Jolyet and Laffont, it contains, in addition, vaso-motor fibres for the mucous membrane of the cheek, lower lip, and their mucous glands; but these fibres are probably derived from the sympathetic.

Trophic Fibres.—As this region of the mucous membrane of the mouth ulcerates after section of the trigeminus, some have supposed that the buccinator nerve contains **trophic fibres.** But, as Rollett pointed out, section of the inferior maxillary nerve paralyses the muscles of mastication on the same side, and hence the teeth do not act vertically upon each other, but press against the cheek. Owing to the loss of the sensibility of the mouth, food passes between the gum and the cheek, where it may remain attached, undergo decomposition, and perhaps chemically irritate the mucous membrane. At a later stage, owing to the wearing away of the teeth in an oblique manner, ulcers begin to form on the *sound* side. Hence, there is no necessity for assuming the existence of tropic fibres in this nerve. After section of the trigeminus, the nasal mucous membrane on the same side becomes red and congested. This is due to the fact that dust or mucus, not being removed from the nose by the usual reflex acts, remains there, irritates, and ultimately causes inflammation.

4. The **lingual nerve** (k) receives at an acute angle the chorda tympani (i i), a branch of the facial coming from the tympanic cavity. The lingual does not contain any motor fibres; it is the **sensory** and **tactile nerve** of the anterior two-thirds of the tongue, of the anterior palatine arch, the tonsil, and the floor of the mouth. These, as well as all the other sensory fibres of the mouth, when stimulated, cause a reflex **secretion of saliva** (compare § 145). The lingual is accompanied by the *nerve of taste* (chorda) for the tip and margins of the tongue (*i.e.*, the parts not supplied by the glosso-pharyngeal). After section of the lingual nerve in man, Busch, Inzani, and Lusanna found that the tactile sensibility was lost in the half of the tongue, and there was loss of taste in the anterior part [two-thirds] of the tongue. The fibres which administer to the sense of taste do not as a rule belong to the lingual itself, but are derived from the *chorda tympani* (p. 735). According to Schiff, the lingual nerve is the gustatory nerve, and some cases of Erb and Senator support this view. Such cases, however, seem to be exceptions to the general rule. The lingual nerve in the substance of the tongue is provided with small ganglia (*Remak*, *Stirling*). Schiff observed that section of the lingual (and also of the hypoglossal) caused *redness of the tongue*, so that vaso-motor fibres are present in its course. It is unknown whether these are derived from the anastomoses of the Gasserian ganglion with the sympathetic. The lingual appears to receive **vaso-dilator fibres** from the chorda for the tongue and gum (§ 349).

After section of the trigeminus, animals frequently bite their tongue, as they cannot feel the position and movement of this organ in the mouth.

5. The **inferior dental** is the **sensory** branch to the teeth and gum of the lower jaw; the vaso-motor fibres reach it from the superior cervical ganglion. Before it passes into the canal in the lower jaw, it gives off the **mylo-hyoid nerve,** which supplies **motor** fibres to the mylo-hyoid and the anterior belly of the digastric, and also some fibres to the triangularis menti and the platysma; the **muscular sensory nerves** also lie in these branches. The mental nerve, which issues from the mental foramen, is the *sensory* nerve for the chin, lower lip, and the skin at the margin of the jaw.

6. The **auriculo-temporal** gives **sensory** branches to the anterior wall of the external auditory meatus, the tympanic membrane, the anterior part of the ear, the adjoining region of the temple, and to the maxillary articulation.

Fig. 519 shows the distribution of the branches of the trigeminus on the head, and the cervical nerves, so that the distribution of anæsthetic and hyperæsthetic areas may easily be made out.

The **otic ganglion** (m) lies beneath the foramen ovale on the inner side of the third divison. Its **roots** are—(1) short **motor fibres** from the third division; (2) **vaso-motor** from the plexus around the middle meningeal artery (ultimately derived from the cervical ganglion of the *sympathetic*); (3) fibres (λ) run from the tympanic branch of the glosso-pharyngeal to the tympanic plexus, and from thence through the canaliculus petrosus in the small superficial petrosal in the cranium, then through a small canal between the apex of the petrous bone and the sphenoid

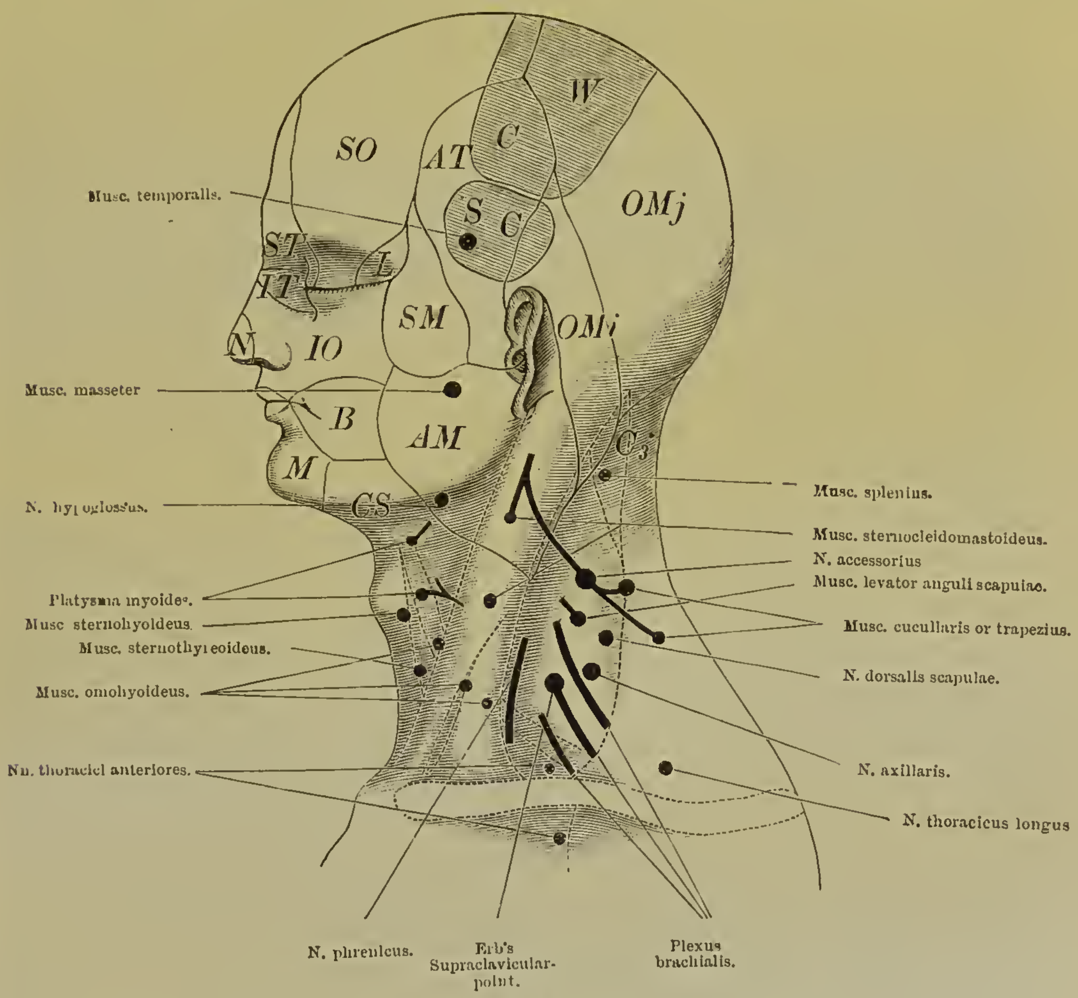


Fig. 519.

Distribution of the sensory nerves on the head as well as the position of the motor points on the neck. *SO*, area of distribution of the supraorbital nerve; *ST*, supratrochlear; *IT*, infratrochlear; *L*, lachrymal; *N*, ethmoidal; *IO*, infraorbital; *B*, buccinator; *SM*, subcutaneous malæ; *AT*, auriculo-temporal; *AM*, great auricular; *OMj*, great occipital; *OMi*, lesser occipital; C_3, three cervical nerves; *CS*, cutaneous branches of the cervical nerves; *C, W*, region of the central convolutions of the brain; *SC*, region of the speech-centre (third left frontal convolution).

to reach the otic ganglion. Through the chorda tympani the facial nerve is constantly connected with the ganglion (fig. 519).

The **branches of the otic ganglion** are—(1) **motor** twigs for the tensor tympani and tensor of the soft palate (these fibres are mixed with muscular sensory fibres—*Ludwig and Politzer*); (2) one or more branches connecting the ganglion with the auriculo-temporal are carried by the roots 2 and 3 from the sympathetic and glosso-pharyngeal, which the auriculo-temporal nerve (Λ), as it passes through the parotid

gland (P), gives off to the gland. These are the **secretory** fibres for the parotid; their functions are stated in § 145.

Section of the trigeminus is followed by inflammatory changes in the tympanic cavity (rabbit); the degree of inflammation varies much (*Berthold and Grünhagen*). Section of the sympathetic or glosso-pharyngeal has no effect.

The **sub-maxillary ganglion** (fig. 518, L) lies close to the convex arch of the tympanico-lingual nerve and the excretory duct of the sub-maxillary gland (M) [in what Langley has called the *chorda-lingual triangle*]. Its **roots** are—(1) branches of the **chorda tympani**, *i i*, which undergo fatty degeneration after section of the facial nerve. This root supplies **secretory fibres** to the sub-maxillary and sub-lingual glands, but it also supplies **vaso-dilator** fibres for the blood-vessels of the same glands (§ 145). In addition, fibres are supplied to the smooth muscular fibres in Wharton's duct. All the fibres of the chorda do not pass into the gland; some pass along with the lingual nerve into the tongue (see *Chorda*, under *Facial Nerve*). (2) The **sympathetic root** of the ganglion arises from the plexus around the submental branch of the external maxillary artery (*q*), *i.e.*, ultimately from the superior cervical ganglion; it passes to the gland, and contains **secretory** fibres, whose stimulation is followed by the secretion of thick concentrated saliva (**trophic** nerve of the gland (?)). It also carries the vaso-constrictor nerves to the gland (§ 144). (3) The **sensory root** springs from the lingual. Some of the fibres, after passing through the ganglion, supply the gland and its excretory ducts, while a few issue from the ganglion, and again join the tympanico-lingual nerve to reach the tongue.

[**Action of Nicotin.**—In the dog and cat Langley has shown that the ganglion which is called the "submaxillary ganglion" in these animals should more properly be called the sub-lingual ganglion, as the chorda tympani has no connection with the nerve-cells of the so-called submaxillary ganglion, so that this ganglion, together with nerve-cells lying near it between the chordo-lingual nerve and Wharton's duct, and also some cells lying outside the hilum of the submaxillary gland, are for the greater part in the course of nerve-fibres to the sub-lingual gland. The real submaxillary ganglion lies in the hilum of the corresponding gland. The sympathetic fibres which pass along the facial artery include some—chiefly fine—medullated nerve-fibres, but the sympathetic nerve-fibres are not connected with the nerve-cells which occur in the course of the chorda tympani; they run along the artery of the gland to the ganglion at the hilum of the submaxillary gland.]

[Experimental evidence supports the above conclusions, based on histological examination, for stimulation of the chordo-lingual and "sub-maxillary ganglion" after section of the chorda near the lingual does not cause secretion, at least to any extent, from the sub-maxillary gland, but it causes slight secretion from the sub-lingual gland. The action of nicotin also confirms the above statements. **Nicotin** paralyses the nerve-cells of various sympathetic ganglia without paralysing the peripheral ends of the nerve-fibres (*Langley and Dickinson*).

If nicotin be injected into the vein of a dog, stimulation of the chordo-lingual nerve causes no secretion either in the sub-lingual or sub-maxillary gland, but if the hilum of the sub-maxillary gland be stimulated, secretion takes place, because the fibres issuing from the sub-maxillary hilum ganglion are excited.]

[After the local application of nicotin to the "sub-maxillary ganglion" and the adjacent ganglionic cells, stimulation of the chordo-lingual nerve causes a secretion in the sub-maxillary gland, but none in the sub-lingual; while the local application of nicotin to the sub-maxillary hilum ganglion prevents the sub-maxillary secretion which, under ordinary circumstances, results from stimulation of the chordo-lingual nerve or chorda tympani. But nicotin thus applied does not affect the secretion obtained from the sub-maxillary gland after stimulation of the **sympathetic fibres**, so that the secretory fibres of the sympathetic are not connected with nerve-cells in the hilum of the gland; they are, as we shall see, connected with nerve-cells in the superior cervical ganglion (§ 356).]

[By the nicotin method of investigation it has been shown that the **vaso-dilator fibres** of the chorda tympani are connected with nerve-cells, but the latter are not so easily paralysed as the peripheral nerve-cells connected with the secretory fibres of the chorda.]

[By the same method Langley has shown that the vaso-constrictor fibres in the cervical sym-

pathetic, and the vaso-dilator fibres in the same trunk, are only connected with nerve-cells in the superior cervical ganglion, and not anywhere else in their course from their origin in the medulla to their ultimate endings.]

Pathological.—Trismus, or *spasm of the muscles of mastication* supplied by the third division, is usually bilateral ; it may be clonic in its nature (chattering of the teeth), or tonic, when it constitutes the condition of lock-jaw or trismus. The spasms are usually individual symptoms of more extensive convulsions ; more rarely when they occur alone, they are symptomatic of disease of the cerebrum, medulla, pons, and cortex of the motor convolutions (*Eulenburg*). The spasms may be caused reflexly, *e.g.*, by stimulation of the sensory nerves of the head.

Paralysis.—Degeneration of the motor nuclei, or an affection of the intracranial root of the nerve, causes paralysis of the muscles of mastication, which is very rarely bilateral. Paralysis of the tensor tympani is said to cause difficulty of hearing (*Romberg*), or buzzing in the ears (*Benedict*). We require further observations upon this point, as well as upon paralysis of the tensor of the soft palate.

Neuralgia may occur in all the branches of the fifth. It consists of severe attacks of pain shooting into the expansions of the nerves. It is usually unilateral, and in fact is often confined to one branch, or even to a few twigs of one branch. The point from which the pain proceeds is frequently the bony canal through which the branch issues. The ear, dura mater, and tongue are rarely attacked. The attack is not unfrequently accompanied by contractions or twitchings of the corresponding group of the facial muscles. The twitchings are either reflex, or are due to direct peripheral irritation of the fibres of the facial nerve, which are mixed with the terminal branches of the trigeminus. The reflex twitchings may be extensively distributed, involving even the muscles of the arm and trunk.

Redness, or congestion of the affected part of the face, is not an unfrequent symptom in neuralgia, and it may be accompanied by increased or diminished secretion from the nasal and buccal mucous membranes. This is a reflex phenomenon, the sympathetic being affected. Reflex stimulation of the vaso-motor nerves frequently gives rise to *disturbance of the cerebral activities*, owing to changes in the distribution of the blood in the head. Ludwig and Dittmar found that stimulation of sensory nerves caused a reflex contraction of the arterial blood-vessels, and increase of the blood-pressure in the cerebral vessels. Sometimes there is melancholy or hypochondriasis, and in one case of violent pain in the inferior maxillary nerve, the attack was accompanied by hallucinations of vision.

The **trophic disturbances** which sometimes accompany affections of the trigeminus are particularly interesting. They are—a brittle character of the **hair**, which frequently becomes grey, or may fall out ; circumscribed areas of **inflammation of the skin**, and the appearance of a vesicular eruption upon the face [often following the distribution of certain nerves], and constituting **herpes**, which may also occur on the cornea, constituting the neuralgic **herpes corneæ** of Schmidt-Rimpler. Lastly, there is the progressive **atrophy of the face** which is usually confined to one side, but may occur on both sides (*Eulenburg*). It is caused very probably by a trophic affection of the trigeminus, although the vaso-motor nerves may also be affected reflexly. Landois found that in the famous case of Romberg, a man named Schwahn, the sphygmographic tracing of the carotid pulse of the atrophied side was distinctly smaller than on the sound side.

Urbantschitsch made the remarkable observation that stimulation of the branches of the trigeminus, especially those going to the ear, caused an **increase of the sensation of light** in the person so stimulated. Blowing upon the cheeks or nasal mucous membrane, electrical stimulation, the use of snuff, smelling strong perfumes—all temporarily increase the sensation of light. The senses of taste and smell, as well as the sensibility of certain areas of the skin, can all be exalted *reflexly* by gentle stimulation of the trigeminus. In intense affections of the ear, whereby the fibres of the trigeminus are often affected sympathetically, these sensory functions may be diminished. As the ear-malady begins to improve, the excitability of these sense organs also again begins to improve.

[**Complete section of the trigeminus** results in loss of sensibility in all the parts supplied by it (fig. 519), including one side of the face, temple, part of the ear, the fore part of the head, conjunctiva, cornea, mouth, gums, Schneiderian mucous membrane, anterior two-thirds of the tongue, and part of pharynx. In drinking from a vessel, the patient feels as if one side of it were cut away. The muscles of mastication are paralysed on that side, food is not chewed on one side, and fur accumulates on the tongue on that side. The mucous membranes tend to ulcerate, that of the mouth being chafed by the teeth, the gums get spongy, the nasal mucous membrane tends to ulcerate, so that smelling is interfered with, and ammonia excites no reflex acts, while the eye undergoes panophthalmia.]

[Gowers is of opinion that the sensation of taste on the posterior part of the tongue, soft palate, and palatine arch depends on the fifth nerve and not on the glosso-pharyngeal nerve.]

348. VI. NERVUS ABDUCENS.—**Anatomical.**—It rises slightly in front of and partly from the nucleus of the *facial nerve* (which corresponds to the anterior horn of the spinal cord), from large-celled ganglia in the deeper part of the anterior region of the fourth ventricle (eminentia teres, figs. 516, 520). [Its nucleus is connected with the nucleus of the third nerve of the opposite side. It appears at the posterior margin of the pons (fig. 517, VI.). This nerve has a very long course before it enters the orbit, and as it bends over the posterior margin of the pons, it is liable to be compressed there or from pressure upon the tentorium cerebelli, so that both nerves are very liable to paralysis.]

Function.—It is the voluntary nerve of the external rectus muscle. In co-ordinated movements of the eyeballs, however, it is involuntary.

Anastomoses.—Branches reach it from the sympathetic upon the cavernous sinus (fig. 518). A few come from the trigeminus, and their function is analogous to similar fibres supplied to the trochlearis and oculomotorius.

Pathological.—Complete **paralysis** causes squinting inwards [or *convergent squint*] and consequent diplopia. [The eye cannot be rotated outwards beyond the middle line, the double images are in the same horizontal plane and vertical, the false one is to the left of the patient's eye when the left eye is affected (fig. 515, 2). The feeling of giddiness is often severe. There is secondary deviation to the inner side, and the head is turned towards the affected side.] In dogs, section of the cervical sympathetic causes a slight deviation of the eyeball inwards (*Petit*). This is explained by the fact that the abducens receives a few motor fibres from the cervical sympathetic. **Spasm** of the abducens causes external squint.

Squint.—In addition to paralysis or stimulation of certain nerves producing squint, it is to be remembered that it may also be caused by a primary affection of the muscles themselves, *e.g.*, congenital shortness, contracture, or injuries of these muscles. It may also be brought about owing to *opacities* of the transparent media of the eye; a person with, say, an opacity of the cornea, rotates the affected eye involuntarily, so that the rays of light may enter the eye through a clear part of the media.

349. VII. NERVUS FACIALIS.—**Anatomical.**—This nerve consists entirely of efferent fibres, and arises from the floor of the fourth ventricle from the "**facial nucleus**" (figs. 516, 7, 520),

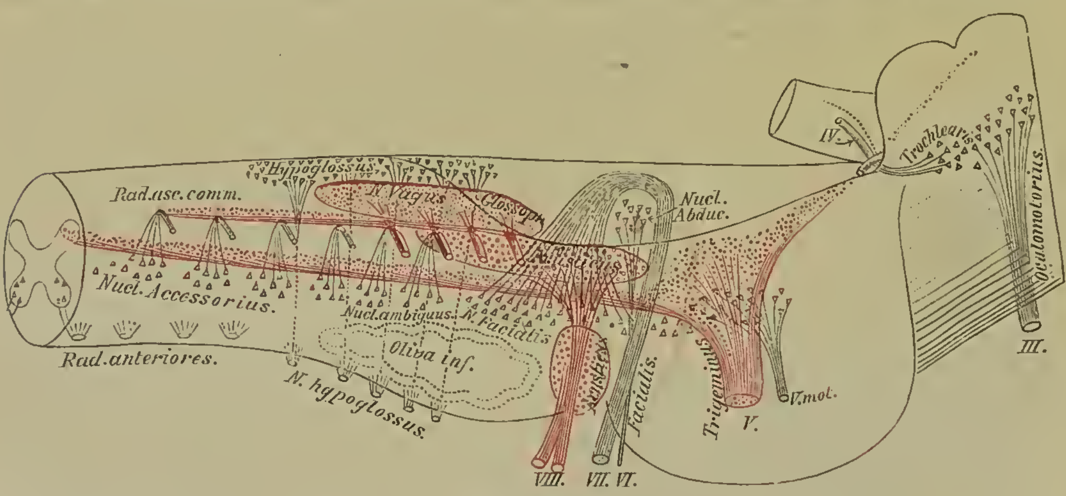


Fig. 520.
Scheme of the disposition of the nuclei of origin of the cranial nerves in the region of the bulb and pons.

which lies behind the origin of the abducens, and also by some fibres from the nucleus of the abducens [although Gowers' observations do not confirm this (§ 366)]. Other fibres arise from the cerebrum of the opposite side (§ 378, I.). It consists of two roots, the smaller—**portio intermedia** of Wrisberg—forms a connection with the auditory nerve (see § 350). The original fibres of the portio intermedia are developed from the glosso-pharyngeal nucleus (*Sapolini*). It would thus appear that the sensory and gustatory fibres which are present in the chorda tympani enter it through these fibres (*Duval, Schultze, Vulpian*), so that the portio intermedia is a special part of the nerve of taste, which becomes conjoined with the facial, and runs to the tongue in the chorda. Along with the auditory nerve, it traverses the porus acusticus internus, where it passes into the facial or Fallopian canal. At first it has a transverse direction as far as the hiatus of this canal; it then bends at an acute angle at the "**knee**" (*a*) above the tympanic

cavity, to descend in an osseous canal in the posterior wall of this space (fig. 518). It emerges from the stylo-mastoid foramen, pierces the parotid gland, and is distributed in a fan-shaped manner (pes anserinus major). [The superficial origin is at the lower margin of the pons, in the depression between the olivary body and the restiform body, as indicated in fig. 517, VII *a*.]

Its **branches** are:—1. The **motor large superficial petrosal** (*j*). It arises from the "knee" or geniculate ganglion within the Fallopian canal, in the cavity of the skull, runs upon the anterior surface of the temporal bone, traverses the foramen lacerum medium on the under surface of the base of the skull, and passes through the Vidian canal to reach the spheno-palatine ganglion (p. 729). It is uncertain whether this nerve conveys **sensory** branches from the second division of the trigeminus to the facial.

2. Connecting branches (β) pass from the geniculate ganglion to the otic ganglion. For their course and function, see *Otic ganglion* (p. 731).

3. The **motor** branch to the **stapedius** muscle (γ).

4. The **chorda tympani** (*i i*) arises from the facial before it emerges at the stylomastoid foramen (*s*), runs through the tympanic cavity (above the tendon of the tensor tympani, between the handle of the malleus and the long process of the incus), passes out of the skull through the petro-tympanic fissure, and then joins the lingual nerve at an acute angle (p. 730, 4). Before it unites with this nerve, it exchanges fibres with the otic ganglion (*m*). Thus, **sensory** fibres can enter the chorda from the third division of the trigeminus, which may run centripetally to the facial to be distributed along with it. In the same way, sensory fibres may pass from the lingual nerve through the chorda into the facial (*Longet*). Stimulation of the chorda—which even in man may be done in cases where the tympanic membrane is destroyed—causes a prickling feeling in the anterior margins and tip of the tongue (*Tröltsch*). O. Wolfe found that the section of the chorda in man abolished the sensibility for **tactile** and **thermal** stimuli upon the tip of the tongue; and the same was true of the sense of **taste** in this region. It is supposed by Calori that these fibres enter the facial nerve at its periphery (especially through the auriculo-temporal into the branches of the facial), that they run in a centripetal direction in the facial, and afterwards pursue a centrifugal course in the chorda. [It is possible that sensory fibres pass from the spheno-palatine ganglion of the fifth through the Vidian nerve and large superficial petrosal to enter the facial. These fibres may be those that appear in the seventh as the chorda fibres which administer to taste. Bigelow asserts that the chorda tympani is not a branch of the facial, but the continuation of the nervus intermedius of Wrisberg.] The chorda also contains **secretory** and **vaso-dilator** fibres for the sub-maxillary and sub-lingual glands (§ 145).

[The chorda is composed of several bundles of medullated nerve-fibres, chiefly small (2·5 to 3·5 μ), mixed with a few medium-sized ones. It has already been pointed out (p. 732) that the secretory and vaso-dilator fibres of the chorda are connected with nerve-cells before they reach their ultimate endings in the glands; the nerve-cells for the sub-lingual gland lying in what is usually called the sub-maxillary ganglion, some cells in the chorda-lingual triangle, and others in the gland itself, while the nerve-fibres of the chorda for the sub-maxillary gland are chiefly connected with the ganglion in the hilum of the sub-maxillary gland.]

Gustatory Fibres.—The chorda also contains fibres administering to the sense of **taste**, for the margin and tip of the tongue (anterior two-thirds), which are conveyed to the tongue along the course of the lingual. Urbantschitsch made observations upon a man whose chorda was freely exposed, and in whom its stimulation in the tympanic cavity caused a sensation of taste (and also of touch) in the margins and tip of the tongue.

It would seem, therefore, that the **gustatory fibres of the chorda** have their

origin in the **glosso-pharyngeal nerve.** They may reach the chorda :—1. Through the portio intermedia of Wrisberg, as already mentioned.

2. There is a channel beyond the stylomastoid foramen, viz., through the ramus communicans cum glosso-pharyngeo (fig. 518), which passes from the last-mentioned nerve in that branch of the facial which contains the motor fibres for the stylohyoid and posterior belly of the digastric muscle (Henle's N. styloideus). This nervo also supplies muscular sensibility to the stylohyoid and posterior belly of the digastric muscles. It is also assumed that, by means of these anastomoses, motor fibres are supplied by the facial to the glosso-pharyngeal nerve. 3. A union of the glosso-pharyngeal and facial nerves occurs in the tympanic cavity. The tympanic branch of the glosso-pharyngeal (λ) passes into this cavity, where it unites in the tympanic plexus with the small superficial petrosal nerve (β), which springs from the knee on the facial. The gustatory fibres may first pass into the otic ganglion, which is always connected with the chorda (Otic ganglion, p. 731, 3). Lastly, a connection is described through a twig (π) from the petrous ganglion of the glosso-pharyngeal, direct to the facial trunk within the Fallopian canal (*Garibaldi*).

According to some observers, the chorda contains **vaso-dilator fibres** for the anterior two-thirds of the tongue (*Vulpian*).

Pseudo-motor Action of the Chorda.—From one to three weeks after the section of the hypoglossal nerve, stimulation of the chorda causes movements in

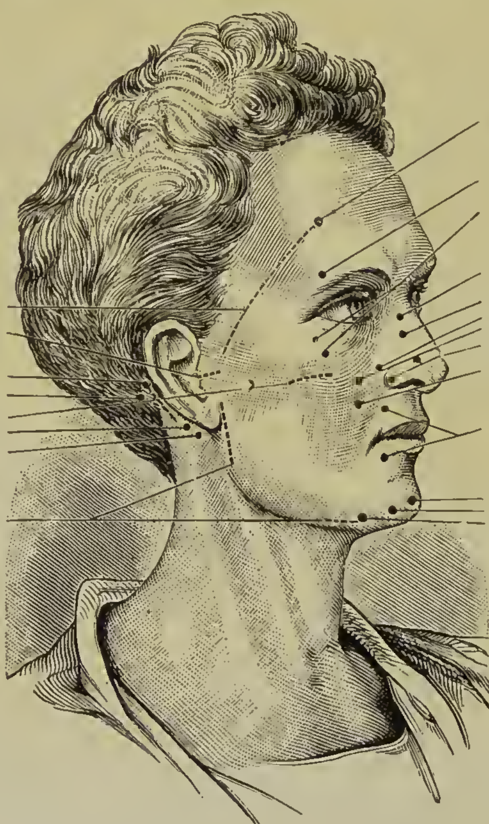


Fig. 521.

Motor points of the facial nervo and tho facial muscles supplied by it.

the tongue (*Philippeaux and Vulpian*). These movements are not so energetic as, and occur more slowly than, those caused by stimulation of the hypoglossal. *Nicotin* first excites, then paralyses, the motor effect of the chorda. Even after cessation of the circulation, stimulation of the chorda causes movements. Heidenhain supposes that, owing to the stimulation of the chorda, there is an increased

secretion of lymph within the musculature, which acts as the cause of the muscular contraction. He called this action "*pseudo-motor*."

[If, after the union of the central end of the lingualis and the peripheral end of the hypoglossal nerve, the lingualis be stimulated, there is a genuine contraction of the musculature of the tongue on that side. A pseudo-motor contraction is easily distinguished from a true contraction, for when a telephone is connected with the tongue, on stimulating the hypoglossal the tone of the tetanus thereby produced is heard, but on stimulating the lingual, although the pseudo-motor contractions occur, no sound is heard (*Rogowicz*).]

5. **Connection with Vagus.**—Before the chorda is given off, the trunk of the facial comes into direct relation with the auricular branch of the vagus (δ), which crosses it in the mastoid canal, and supplies it with sensory nerves (see *Vagus*).

6. **Peripheral Branches.**—After the facial issues from its canal, it supplies **motor fibres** to the stylohyoid and posterior belly of the digastric, occipitalis, all the muscles of the external ear, the muscles of expression, buccinator and platysma. The facial also contains **secretory fibres** for the face (compare § 288).

Although most of the branches of the facial are under the influence of the will, yet most men cannot voluntarily move the muscles of the nose and ear.

Anastomoses of the Facial nerve.—The branches of the seventh nerve on the face anastomose with those of the trigeminus, whereby sensory fibres are conveyed to the muscles of expression. The sensory branches of the auricular branch of the vagus, and the great auricular, enter the peripheral ends of the facial, and supply sensibility to the muscles of the ear; while the sensory fibres of the third cervical nerve similarly supply the platysma with sensibility. Section of the facial at the stylomastoid foramen is painful, but it is still more so if the peripheral branches on the face are divided (*Recurrent sensibility*, § 355).

Pathological.—In all cases of paralysis of the facial, the most important point to determine is whether the seat of the affection is in the periphery, in the region of the stylomastoid foramen, or in the course of the long Fallopian canal, or is central (cerebral) in its origin. This point must be determined by an analysis of the symptoms. Paralysis at the stylomastoid foramen is very frequently rheumatic, and probably depends upon an exudation compressing the nerve; the exudation probably occupying the lymph-space described by Rüdinger on the inner side of the Fallopian canal, between the periosteum and the nerve, and which is a continuation of the arachnoid space. Other causes are—inflammation of the parotid gland, direct injury, and pressure from the forceps during delivery. In the **course of the canal**, the causes are—fracture of the temporal bone, effusion of the blood into the canal, syphilitic effusions, and caries of the temporal bone; the last sometimes occurs in inflammation of the ear. Amongst **intracranial causes** are—affections of the membranes of the brain, and of the base of the skull in the region of the nerve, disease of the "**facial nucleus**;" lastly, affection of the cortical centre of the nerve and its connections with the nucleus. [No nerve is so liable as the seventh to be paralysed independently.]

Symptoms of Unilateral Paralysis of the Facial [or Bell's Paralysis].—1. Paralysis of the **muscles of expression**: The forehead is smooth, without folds, the eyelids remain open (**lagophthalmus paralyticus**), the outer angle being slightly lower. The anterior surface of the eye rapidly becomes dry, the cornea is dull, as, owing to the paralysis of the orbicularis, the tears are not properly distributed over the conjunctiva, and, in fact, in consequence of the dryness of the eyeball, there may be temporary inflammation (**keratitis xerotica**). In order to protect the eyeball from the light, the patient turns it upwards under the upper eyelid (*Bell*), relaxes the levator palpebræ, which allows the lid to fall somewhat (*Hasse*). The nose is immovable, while the naso-labial fold is obliterated. As the nostrils cannot be dilated, the sense of smell is interfered with. The impairment of the **sense of smell** depends more, however, upon the imperfect conduction of the tears, owing to paralysis of the orbicularis palpebrarum and Horner's muscle, thus causing dryness of the corresponding side of the nasal cavity. Horses, which distend the nostrils widely during respiration, after section of both facial nerves, are said by Cl. Bernard to die from interference with the respiration, or at least they suffer from severe dyspnœa (*Ellenberger*). The face is drawn towards the sound side, so that the nose, mouth, and chin are oblique. Paralysis of the buccinator interferes with the proper formation of the **bolus of food**; the food collects between the cheek and the gum, from which it is usually removed by the patient with his fingers; saliva and fluids escape from the angle of the mouth. During vigorous expiration the cheeks are pulled outwards like a sail. The speech may be affected owing to the difficulty of sounding the **labial consonants** (especially in double paralysis), and the vowels, u, ü (ue), ö (oe); whilo tho speech, in paralysis of the branches to

both sides of the palate, becomes nasal (§ 628). The acts of whistling, sucking, blowing, and spitting are interfered with. In **double paralysis**, many of these symptoms are greatly intensified, while others, such as tho oblique position of the features, disappear. The features are completely relaxed ; there is no mimetic play of the features, the patients weep and laugh, "as it were, behind a mask" (*Romberg*). 2. In **paralysis of the palate**, when the uvula is directed towards the sound side, and the paralysed half of the palate hangs down and cannot be raised (large superficial petrosal nerve), it is not determined to what extent this condition influences the *act of deglutition* and the *formation of the consonants*. 3. **Taste** is interfered with ; either it is absent on the anterior two-thirds of the tongue, or the sensation is delayed and altered. This is due to an affection of the chorda. 4. **Diminution of saliva** on the affected side was first described by Arnold ; still, we must determine to what extent a simultaneous affection of the sense of taste may cause a reflex interference with the secretion of saliva, or whether rapid removal of the saliva through the opened lips and angle of the mouth may cause the dryness on the affected side of the mouth. 5. Roux pointed out that **hearing** is affected, the *sensibility to sounds* being increased (**oxyakoia, hyperakusis willisiana**). The paralysis of the stapedius muscle makes the stapes loose in the fenestra ovalis, so that all impulses from the tympanum act vigorously upon the stapes, which consequently excites considerable vibrations in the fluid of the inner ear. More rarely, in paralysis of the stapedius, it has been observed that low notes are heard at a greater distance than on the sound side (*Lucae, Mow*). 6. As the facial in man appears to contain fibres for the **secretion of sweat**, this explains the loss of the power of sweating in the face when the nerve begins to atrophy (*Strauss, Bloch*).

Section of the facial in young animals causes atrophy of the corresponding *muscles*. The **facial bones** are also imperfectly developed ; they remain smaller, and hence the bones of the sound side of the face grow towards, and ultimately across, the middle line towards the affected side (*Brown-Séquard*). The **salivary glands** also remain smaller.

Stimulation—or irritation in the area of the **facial**—causes partial or extensive, either direct or reflex, tonic or clonic spasms. The extensive forms are known as "**mimetic facial spasm.**" Amongst the partial forms are *tonic contraction of the eyelid* (**blepharospasm**), which is most common ; and is caused reflexly by stimulation of the sensory nerves of the eye, *e.g.*, in scrofulous ophthalmia, or from excessive sensibility of the retina (**photophobia**). More rarely, the excitement proceeds from some more distant part, *e.g.*, in one case recorded by v. Gräfe, from inflammatory stimulation of the anterior palatine arch. The centre for the reflex is the facial nucleus. The clonic form of spasm—*spasmodic winking* (**spasmus nictitans**)—is usually of reflex origin, due to irritation of the eye, the dental nerves, or even of more distant nerves. In severe cases, the affection may be bilateral, and the spasms may extend to the muscles of the neck, trunk, and upper extremities. Contraction of the muscles of the lip may be excited by emotions (rage, grief), or reflexly. Fibrillar contractions occur after section of the facial as a "degeneration-phenomenon" (p. 590). [If the facial be torn out at the stylomastoid foramen, there is paralytic oscillation of the lip muscles (*Schiff*). If, in such an animal, the posterior root of the annulus of Vieussens be stimulated electrically, as it contains vaso-dilator fibres (*Dastre and Morat*), not only do the blood-vessels of the cheek and lips dilate, but the veins pulsate and florid blood escapes from the veins, just as occurs in the sub-maxillary gland when the chorda is stimulated. On stimulating the ansa, after section of the seventh, there is a **pseudo-motor effect** on the muscles of the cheek and lips, so that there is an analogy between the chorda and the ansa (*Rogowicz*).] *Intracranial* stimulation of the most varied description may cause spasms. Lastly, facial spasm may be part of a general spasmodic condition, as in epilepsy, chorea, hysteria, tetanus. Aretaeus (81 A.D.) made the interesting observation that the muscles of the ear contracted during tetanus. Very rarely have spasmodic elevation of the palate and increased salivation been described as the result of irritation of the facial (*Leube*). Moos observed a profuse secretion of saliva on stimulating the chorda during an operation on the tympanic cavity.

350. **VIII. NERVUS ACUSTICUS**—Arises by **two roots** (*Stieda*) ; a larger anterior with coarser fibres and a smaller posterior one with finer fibres. From the former proceeds the vestibular nerve, and from the latter the **cochlear nerve** ; these are separated in the sheep and horse (*Horbaczewski*). Each root springs from a median and a lateral nucleus, so that there are four nuclei (fig. 520). Tho **vestibular branch** is chiefly connected with the grey matter in relation with the **cerebellum**, and these fibres may be connected with **equilibration.** The chief mass of the **cochlear nerve** crosses to the other side and passes to the posterior part of the corpora quadrigemina, the internal geniculate body, and finally to the temporo-sphenoidal lobe of the cerebrum (§ 378, IV., 2). After extirpation of the temporo-sphenoidal lobe, these fibres atrophy into the internal capsule and internal geniculate body (*v. Monakow*). The **striæ acusticæ** form a second decussating projection system like a chiasma. The origin of both acoustic nerves are connected by commissures in the brain (*Flechsig*).

In the course of the internal auditory meatus, the auditory and portio intermedia of the facial exchange fibres, but the physiological significance of this is unknown.

Function.—The acusticus or auditory nerve has a **double function**:—1. It is

the **nerve of hearing**; when stimulated, either at its origin, in its course, or at its peripheral terminations, it gives rise to *sensations of sound*. Every *injury*, according to its intensity and extent, causes hardness of hearing or even deafness.

2. Quite distinct from the foregoing is the other function, which depends upon the **semicircular canals**, viz., that stimulation of the peripheral expansions in the ampullæ influences the movements necessary for maintaining the **equilibrium** of the body.

Brenner's Formula.—The relation of the auditory nerve to the galvanic current is very important. In healthy persons, when there is closure at the cathode, there is the sensation of a *clang* (or tone) in the ear, which continues with variations while the current is closed. When the anode is opened, there is a feebler tone (*Brenner's Normal Acoustic Formula*). This clang coincides exactly with the resonance fundamental tone of the sound-conducting apparatus of the ear itself.

Pathological.—*Increased sensibility* of the auditory nerve in any part of its course, its centre, or peripheral expansions causes the condition known as **hyperakusis**, which usually is a sign of greatly increased nervous excitability, as in hysteria. When excessive, it may give rise to distinctly painful impressions, which condition is known as **acoustic hyperalgia** (*Eulenburg*). **Stimulation** of the parts above named causes sensations of sound, the most common being the sensation of *singing in the ears*, or **tinnitus**. This condition is often due to changes in the amount of blood in the blood-vessels of the ear—either anæmic or hyperæmic stimulation. There is well-marked tinnitus after large doses of quinine or salicin, due to the vaso-motor effect of these drugs upon the vessels of the labyrinth (*Kirchner*). Not unfrequently, in cases of tinnitus, the reaction due to the galvanic current is often increased. More rarely there is the so-called "*paradoxical reaction*"—*i.e.*, on applying the galvanic current to one ear, in addition to the reaction in this ear, there is the opposite result in the non-stimulated ear. In other cases of disease of the auditory nerve, noises rather than musical notes are produced by the current; *stimulation*, especially of the cortical centre of the auditory nerve, chiefly in lunatics, may cause **auditory delusions** (§ 378, IV.). According as the excitability of the auditory nerve is diminished or abolished, there is the condition of nervous hardness of hearing (**hypakusis**), or nervous deafness (**anakusis**).

The Semicircular Canals of the Labyrinth.—Section or injury to these canals does not interfere with hearing, but other important symptoms follow their injury, such as disturbances of equilibrium due to a feeling of giddiness, especially when the injury is bilateral (*Flourens*). This does not occur in fishes (*Kiesselbach*). The **pendulum-like movement of the head**, in the direction of the plane of the injured canal, is very characteristic. If the *horizontal* canal be divided, the head (of the pigeon) is turned alternately to the right and left. The rotation takes place, especially when the animal is about to execute a movement; when it is at rest, the movement is less pronounced. The phenomenon may last for months, and injury to the *posterior vertical* canals causes a well-marked up and down movement or nodding of the head, the animal itself not unfrequently falling forwards or backwards. Injury to the *superior vertical* canals also causes pendulum-like vertical movements of the head, while the animal often falls forwards. When *all the canals* are destroyed, various pendulum-like movements are performed, while standing is often impossible. Breuer found that electrical stimulation of the canals caused rotation of the head, while Landois on applying a solution of salt to the canals, observed pendulum-like movements, which, however, disappeared after a time. A 25 per cent. solution of chloral dropped into the ear of a rabbit causes, after fifteen minutes, similar effects to destruction of the canals (*Vulpian*). Section of the acoustic nerves within the cranium has the same result (*Bechterew*).

[From the foregoing and other experiments there seems to be no doubt that the semicircular canals and the impressions proceeding from them, form a most important part of the afferent mechanism of **equilibration**. Marked disturbances of equilibrium take place in all animals after section of the auditory nerve, or destruction of the semicircular canals, the effects being most marked and persistent when the canals on both sides are destroyed, so that it may be taken that certain disturbances of equilibrium stand in causal relation to lesions of the semicircular canals. The other

effects associated with injury of these canals are **movements of the head** in the plane of the injured canal, and movements of the **eyeballs.** These organs seem to be in no way associated with hearing. Animals with their semicircular canals destroyed still hear by means of aerial vibrations, while an animal without its cochlea is deaf, but its equilibration is not thereby affected.]

Explanation.—Goltz regards the canals as organs of sense for ascertaining the equilibrium or position of the head in space; Mach as an organ for ascertaining the movements of the head. According to Goltz's **statical theory**, every position of the head causes the endolymph to exert the greatest pressure upon a certain part of the canals, and thus excites in a varying degree the nerve-terminations in the ampullæ. According to Breuer, when the head is rotated, currents are produced in the endolymph of the canals, which must have a fixed relation to the direction and extent of the movements of the head, and these currents, therefore, when they are perceived, afford a means of determining the movement of the head. The nervous end-organs of the ampullæ are arranged for ascertaining this perception. If the semicircular canals are an apparatus—in fact, "sense-organs"—for the sensation of the equilibrium, and if their function is to determine the position or movements of the head, necessarily their destruction or stimulation must alter these perceptions, and so give rise to abnormal movements of the head. Vulpian regards the rotation of the head as due to strong auditory perceptions (?) in consequence of affections of the canals. Böttcher, Tomaszewicz, and Baginsky regard the injury to the cerebellum as the cause of the phenomena. The pendulum-like movements, however, are so characteristic that they cannot be confounded with disturbances of the equilibrium which result from injury to the cerebellum.

[**Kinetic Theory.**—In 1875 Crum Brown pointed out that if a person be rotated passively, his eyes being bandaged, he can, up to a certain point, indicate pretty accurately the amount of movement, but after a time this cannot be done, and if the rotation, as on a potter's wheel, be stopped, the sense of rotation continues. Crum Brown suggested that currents were produced in the endolymph, while the terminal hair-cells lagged behind, and were, in fact, dragged through the fluid. He pointed out that the right posterior canal is in line with the left superior, and the left posterior with the right superior, a fact which is readily observed by looking from behind at a skull, with the semicircular canals exposed (fig. 522). He assumes that the canals are paired organs, and that each pair is connected with rotation or movement of the head in a particular direction.]

Giddiness.—This feeling of false impressions as to the relations of the surroundings and consequent movements of the body, occurs especially during *acquired* changes in the normal movements of the eyes, whether due to involuntary to and fro movements of the eyeballs (**nystagmus**), or to paralysis of some eye muscle.

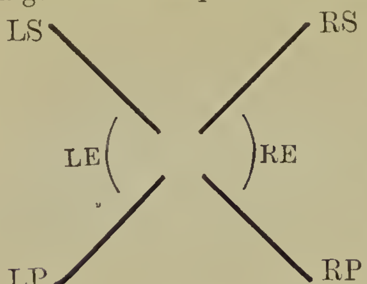


Fig. 522.

Diagram of the disposition of the semicircular canals. RS and LS, right and left superior; LP and RP, right and left posterior; LE and RE, right and left external.

Active or passive movements of the head or of the body are normally accompanied by simultaneous movements of both eyeballs, which are characteristic for every position of the body. The general character of these "compensatory" bilateral movements of the eyes consists in this, that during the various changes in the position of the head and body, the eyes strive to maintain their primary passive position. Section of the aqueduct of Sylvius at the level of the corpora quadrigemina, of the floor of the fourth ventricle, of the auditory nucleus, both acustici, as well as destruction of both membranous labyrinths, causes disappearance of these movements; while, conversely, stimulation of these parts is followed by bilateral associated movements of the eyeballs.

Compensatory movements of the eyeballs, under normal circumstances, may be caused reflexly from the membranous labyrinth. Nerve channels, capable of exciting reflex movements of both eyes, proceed from both labyrinths, and, indeed, both eyes are affected from both labyrinths. These channels pass through the auditory nerve to the *centre* (nuclei of the 3rd, 4th, 6th, and 8th cranial nerves), and from the latter efferent fibres pass to the muscles of the eye (*Högyes*).

Effects of Section of the Canals.—Cyon found that stimulation of the horizontal semicircular canal was followed by horizontal nystagmus; of the posterior, by vertical, and of the anterior canal, by diagonal nystagmus. Stimulation of one auditory nerve is followed by rotating nystagmus, and rotation of the body of the animal on its axis towards the stimulated side.

Drugs.—Chloroform and other poisons enfeeble the compensatory movements of the eyeballs, while nicotin and asphyxia suppress them, owing to their action on their nerve-centre.

It is probable that the disturbances of equilibrium and the feeling of giddiness which follow the passage of a galvanic current through the head between the mastoid processes, are also due to an action upon the semicircular canals of the labyrinth (§ 300). Deviation of the eyeballs is produced by such a galvanic current (*Hitzig*). The same result is produced when the two electrodes are placed in the external auditory meatuses.

Pathological.—Menière's Disease.—The feeling of giddiness, not unfrequently accompanied by tinnitus, which occurs in Menière's disease, must be referred to an affection of the nerves of the ampullæ or their central organs, or of the semicircular canals themselves. By injecting fluid violently into the ear of the rabbit, giddiness, with nystagmus and rotation of the head towards the side operated on, are produced (*Baginsky*). In cases in man, where the tympanic membrane was defective, Lucæ, when employing the so-called ear-air-douche at 0·1 atmosphere, observed abduction of the eyeball with diplopia, giddiness, darkness in front of the eyes, while the respiration was deeper and accelerated. These phenomena must be due to stimulation or exhaustion of the vestibular branch of the auditory nerve (*Högyes*). In chronic gastric catarrh, a tendency to giddiness is an occasional symptom (Trousseau's gastric giddiness). This may perhaps be caused by stimulation of the gastric nerves exciting the vaso-motor nerves of the labyrinth, which must affect the pressure of the endolymph. Analogous giddiness is excited from the larynx (*Charcot*), and from the urethra (*Erlenmeyer*).

[**Vertigo** or **giddiness** is a very common symptom in disease, and may be produced by a great many different conditions. It literally means "a turning." As Gowers points out, the most common symptom is that the patient himself has a sense of movement in one or other direction; or objects may appear to move before him; and more rarely there is actual movement, "commonly in the same direction as the subjective sense of movement." It is sometimes due to a want of harmony between the impressions derived from different sense-organs or "contradictoriness of sensory impressions" (*Grainger Stewart*), as is sometimes felt on ascending or descending a stair, or by some persons while standing on a high tower, constituting tower or cliff giddiness. One of the most remarkable conditions is that called "**agoraphobia**" (*Benedikt, Westphal*). The person can walk quite well in a narrow lane or street, but when he attempts to cross a wide square, he experiences a feeling closely allied to giddiness. The giddiness of sea-sickness is proverbial, while some persons get giddy with waltzing or swinging. Besides occurring in Menière's disease, it sometimes occurs in locomotor ataxia, and some cerebral and cerebellar affections, including cerebral anæmia. Very distressing giddiness and headache are often produced by paralysis of some of the ocular muscles, *e.g.*, the external rectus, *i.e.*, **ophthalmic vertigo.** Defective or perverted ocular impressions, as well as similar auditory impressions, may give rise to vertigo; in the latter or labyrinthine form the vertigo may be very severe. Severe vertigo is often accompanied by vomiting. A hard plug of ear-wax may press on the membrana tympani and cause severe giddiness. Vertigo depending on conditions in the ear is **aural vertigo.** The forms of dyspeptic giddiness and the toxic forms due to the abuse of alcohol, tobacco, and some other drugs are familiar examples of this condition.]

[**Tinnitus Aurium**, or subjective noises in the ear, is a very common symptom in disease of the ear, and may be caused by very varied conditions; the noise may be continuous or discontinuous, be buzzing, singing, or rumbling in character.]

351. **IX. NERVUS GLOSSO-PHARYNGEUS.—Anatomical.**—This nerve (figs. 518, 9, 520) arises from the nucleus of the same name, which consists partly of large cells (motor) and partly of small cells (belonging to the gustatory fibres). The nucleus lies in the lower half of the fourth ventricle, deep in the medulla oblongata, near the olive (figs. 516, 520), and posteriorly it abuts on that of the vagus. The anterior part of the central nucleus is regarded as the root of the portio intermedia of the facial (§ 349). The nerve also receives fibres from the vagal centres. The fibres collect into two trunks, which afterwards unite and leave the medulla oblongata in front of the vagus. In the fossula petrosa it has on it the **petrous ganglion**, from which, occasionally, a special part on the posterior twig is separated within the skull, as the ganglion of Ehrenritter. *Communicating branches* are sent from the petrous ganglion to the trigeminus, facial (ϵ and π) vagus and carotid plexus. From this ganglion also the tympanic nerve (λ) ascends vertically in the tympanic cavity, where it unites with the tympanic plexus. This branch (§ 349, 4) gives *sensory* fibres to the tympanic cavity and the Eustachian tube; while, in the

dog, it also carries secretory fibres for the parotid into the small superficial petrosal nerve (*Heidenhain*—§ 145).

Functions.—1. It is the **nerve of taste** for the posterior third of the tongue, the lateral part of the soft palate, and the glosso-palatine arch (compare § 422).

The nerve of taste for the anterior two-thirds of the tongue is referred to under the lingual (§ 347, III, 4) and chorda tympani nerves (§ 349, 4). The glossal branches are provided with ganglia, especially where the nerve divides at the base of the circumvallate papillæ (*Remak, Kölliker, Stirling*). The nerve ends in the circumvallate papillæ (fig. 429, U), and the end-organs are represented by the taste bulbs (§ 423).

2. It is the **sensory nerve** for the posterior third of the tongue, the anterior surface of the epiglottis, the tonsils, the anterior palatine arch, the soft palate, and a part of the pharynx. From this nerve there may be discharged *reflexly* movements of the palate and pharynx, which may pass into those of vomiting (§ 158). These fibres, like the gustatory fibres, can excite a reflex secretion of saliva (§ 145).

3. It is **motor** for the stylo-pharyngeus and middle constrictor of the pharynx (*Volkmann*); and, according to other observers, to the (?) glosso-palatinus (*Hein*) and the (? ?) levator veli palatini and azygos uvulæ (compare *Spheno-palatine ganglion*, § 347, II.). It is doubtful whether the glosso-pharyngeal nerve is really a motor nerve at its origin—although Meynert and others have described a motor nucleus—or whether the motor fibres reach the nerve at the petrous ganglion, through the communicating branch from the facial.

[4. It is the **inhibitory nerve** for the act of **deglutition** (p. 271).]

5. A twig accompanies the lingual artery; this nerve, perhaps, is **vaso-dilator** for the lingual blood-vessels.

Pathological.—There are no satisfactory observations on man of uncomplicated affections of the glosso-pharyngeal nerve.

352. X. NERVUS VAGUS.—**Anatomical.**—The nucleus from which the vagus arises along with the 9th and 11th nerve is in (1) the **ala cinerea** in the lower half of the calamus scriptorius (fig. 516, 10) [and it is very probably the representative of the cells of the vesicular column of Clarke (§ 366)]. (2) Other fibres come from the "**longitudinal bundle**" or "**respiratory bundle**" lying outside the nucleus, and reaching down into the cervical enlargement. (3) A **motor nucleus**—the nucleus ambiguus—a prolongation of some of the cells of the anterior horn of the spinal cord, gives some motor fibres (fig. 520). It leaves the medulla oblongata by 10 to 15 threads behind the 9th nerve, between the divisions of the lateral column, and has a ganglion (**jugular**) upon it in the jugular foramen (fig. 517, VIII). Its branches contain fibres which subserve different functions [see also p. 750].

1. The **sensory meningeal branch** from the jugular ganglion accompanies the vaso-motor fibres of the sympathetic on the middle meningeal artery, and sends fibres to the occipital and transverse sinus.

When it is irritated, as in congestion of the head and inflammation of the dura mater, it gives rise to *vomiting*.

2. The **auricular branch** (fig. 523, *au.*) from the jugular ganglion receives a communicating branch from the petrous ganglion of the 9th nerve, traverses the canaliculus mastoideus, crossing the course of the facial, with which it exchanges fibres whose function is unknown. On its course, it gives **sensory** branches to the posterior part of the auditory meatus, and the adjoining part of the outer ear. A branch runs along with posterior auricular branch of the facial, and confers **sensibility** on the muscles.

When this nerve is irritated, either through inflammation or by the presence of foreign bodies in the outer ear passage, it may give rise to *vomiting*. Stimulation of the deep part of the external auditory meatus in the region supplied by the auricular branch causes *coughing* reflexly [*e.g.*, from the presence of a pea in the ear]. Similarly, *contraction of the blood-vessels of the ear* may be caused reflexly (*Snellen, Lovén*).

The nerve is the remainder of a considerable branch of the vagus which exists in fishes and the larvæ of frogs, and runs under the skin along the side of the body.

3. The **connecting branches** of the vagus are :—(1) A branch which directly connects the petrous ganglion of the 9th with the jugular ganglion of the 10th; its function is unknown. (2) Directly above the plexus gangliiformis vagi, the vagus is joined by the whole inner half of the *spinal accessory.* This nerve conveys to the vagus the **motor** fibres for the *larynx*, and the *cervical part of the œsophagus* (which according to Steiner lie in the inner part of the nerve-trunk), as well as the **inhibitory fibres** for the *heart* (*Cl. Bernard*). (3) The plexus gangliiformis fibres, whose function is unknown, join the trunk of the vagus from the hypoglossal, superior cervical ganglion of the sympathetic, and the cervical plexus.

4. **Pharyngeal Plexus.**—The vagus sends one or two branches (fig. 523, 2) from the upper part of the plexus gangliiformis to the *pharyngeal plexus*, where at the level of the middle constrictor of the pharynx, it is joined by the pharyngeal branches of the 9th nerve and those of the upper cervical sympathetic ganglion, near the ascending pharyngeal artery, to form the *pharyngeal plexus.* The vagal fibres in this plexus supply the *three constrictors of the pharynx* with **motor fibres**, while the tensor palati (*Otic ganglion*, § 347, III.) and levator of the soft palate (compare *Spheno-palatine ganglion*, § 347, II.) also receive motor (? sensory) fibres. **Sensory fibres** of the vagus from the pharyngeal plexus supply the pharynx from the part beneath the soft palate downwards. These fibres excite the pharyngeal constrictors reflexly, during the act of swallowing (§ 156). If stimulated very strongly, they may cause *vomiting.* (The *sympathetic* fibres of the œsophageal plexus give vaso-motor nerves to the œsophageal vessels; for the œsophageal branches of the 9th nerve see above.)

5. The vagus supplies two branches to the larynx, the **superior** and **inferior laryngeal.**

(*a*) The **superior laryngeal** receives **vaso-motor** fibres from the superior cervical ganglion of the sympathetic (fig. 523, 3). It divides into two branches, external and internal :—(1) The **external branch** receives **vaso-motor** fibres from the same source (they accompany the superior thyroid artery), and supply the crico-thyroid muscle with **motor** fibres, and **sensory** fibres to the lower lateral portion of the laryngeal mucous membrane. (2) The **internal** branch gives off *sensory* branches only to the glosso-epiglottidean fold, and the adjoining lateral region of the root of the tongue, the aryepiglottidean fold, and to the whole anterior part of the larynx, except the part supplied by the external branch (*Longet*). Stimulation of any of these sensory fibres causes **coughing** reflexly. **Coughing** is produced by stimulation of the boundaries of the glottis respiratoria, but not of the vocal cords, and by stimulation of the sensory branches of the vagus to the tracheal mucous membrane, especially at the bifurcation, and also from the bronchial mucous membrane (*Kohts*). Coughing is also caused by stimulation of the auricular branch of the vagus, especially in the deep part of the external auditory meatus, of the pulmonary tissue, especially when altered pathologically; in pathological conditions (inflammation) of the pleura (? certain changes in the stomach [stomach-cough]), of the liver and spleen (fig. 165). The **coughing centre** is said to lie on each side of the raphe, in the neighbourhood of the ala cinerea (*Kohts*). Cases of violent coughing may, owing to stimulation of the pharynx, be accompanied by **vomiting** as an associated movement (§ 120).

In many individuals, **coughing** can be excited by stimulation of distant sensory nerves (§ 120, 1), *e.g.*, from the outer ear (auricular nerve), nasal mucous membrane, liver, spleen, stomach, intestine, uterus, mammæ, ovaries, and even from certain cutaneous areas (*Ebstein*). It is uncertain if these conditions act directly upon the coughing centre, or first of all affect the vascularisation and secretion of the respiratory organs, which in their turn affect the coughing centre.

The cough (dog, cat) caused by stimulation of the trachea and bronchi occurs at once, and lasts as long as the stimulus lasts; in stimulation of the larynx, the first effect is inhibition of the respiration accompanied by movements of deglutition, while the cough occurs after the cessation of the stimulation (*Kandarazky*).

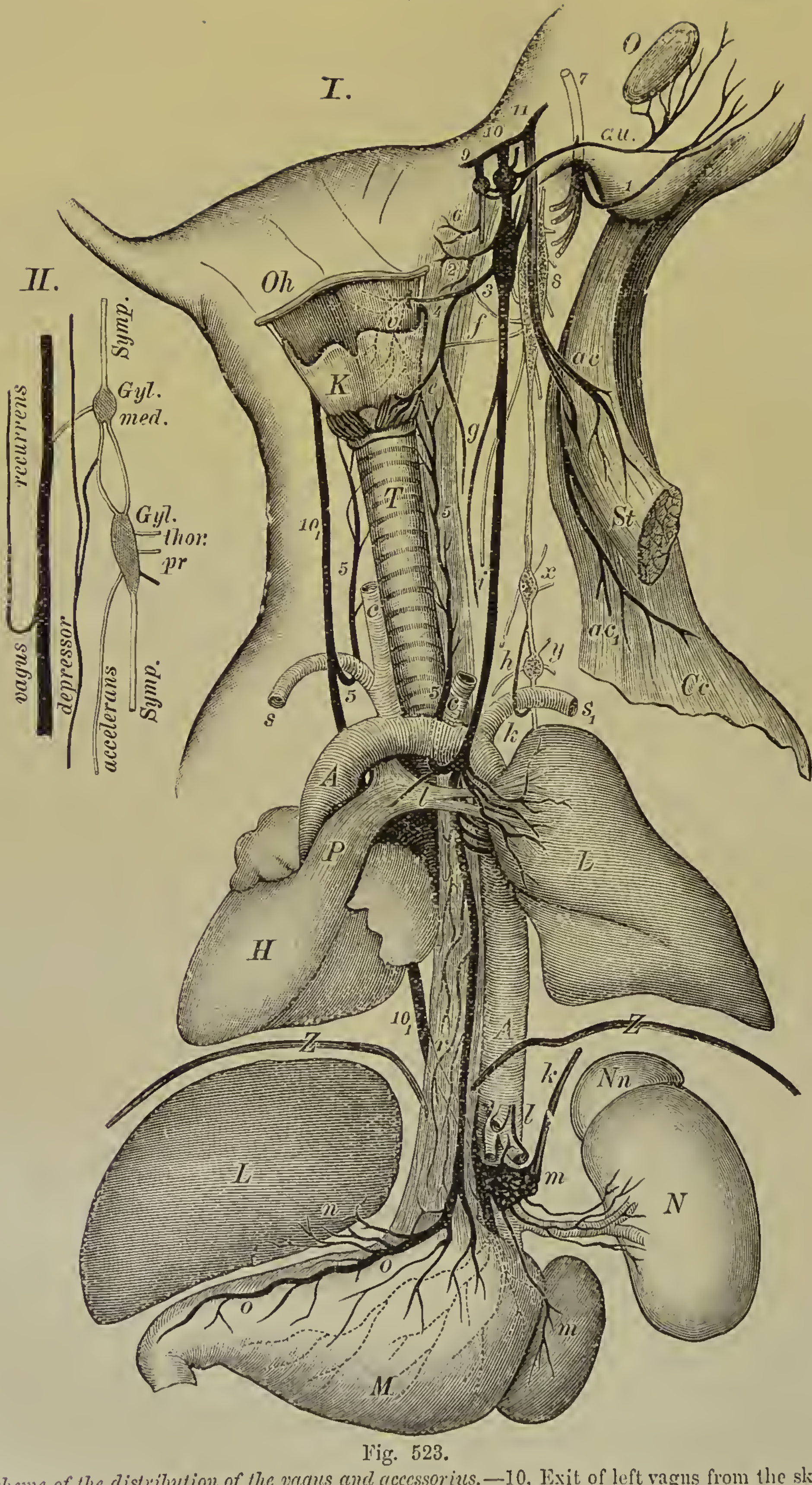


Fig. 523.

I. *Scheme of the distribution of the vagus and accessorius.*—10, Exit of left vagus from the skull; 10_1, right vagus; 9, glosso-pharyngeal; 7, facial; 1, deep post-auricular from the facial;

The **superior laryngeal** contains afferent fibres which, when stimulated, cause **arrest of the respiration** and closure of the rima glottidis (*Rosenthal*)—see *Respiratory centre*, § 368), and fibres which discharge movements of **deglutition**, (p. 270). Lastly, fibres which are efferent and serve to excite the vaso-motor centre, and are in fact "**pressor fibres**"—(see *Vaso-motor centre*, § 371, II.).

(*b*) The **inferior laryngeal** or **recurrent nerve** bends on the left side around the arch of the aorta, and on the right around the subclavian artery, and ascends in the groove between the trachea and œsophagus, giving *motor* fibres to these organs, and the lower constrictors of the pharynx, and passes to the larynx, to supply **motor fibres** to all its muscles, except the cricothyroid. It also has an inhibitory action upon the respiratory centre (see § 368).

A **connecting branch** runs from the superior laryngeal to the inferior (the anastomosis of Galen), which occasionally gives off *sensory* branches to the upper half of the trachea (sometimes to the larynx ?) ; perhaps also to the œsophagus (*Longet*), and sensory fibres (?) for the muscles of the larynx supplied by the recurrent laryngeal. According to François Franck, sensory fibres pass by this anastomosis from the recurrent into the superior laryngeal. According to Waller and Burckhard, the motor fibres of both laryngeal nerves are all derived from the accessorius ; while Chauveau maintains that the cricothyroid is an exception.

Stimulation of the **superior laryngeal** is painful, and causes contraction of the cricothyroid muscle (while the other laryngeal muscles contract *reflexly*). **Section** of both nerves, owing to paralysis of the cricothyroids, causes slight slowing of the respirations (*Sklarek*). In dogs, the voice becomes deeper and hoarser, owing to diminished tension of the vocal cords (*Longet*). The larynx becomes insensible, so that saliva and particles of food pass into the trachea and lungs, without causing reflex contraction of the glottis or coughing. This excites "traumatic pneumonia," which results in death. Unilateral section is followed by unilateral atrophy of the laryngeal muscles (p. 637).

Stimulation of the recurrent nerves causes *spasm of the glottis*. **Section** of these nerves paralyses the laryngeal muscles supplied by them, the voice becomes husky and hoarse (in the pig—*Galen*, *Riolan*, 1618) in man, dog, and cat; while rabbits retain their shrill cry. The glottis is small, with every inspiration, the vocal cords approximate considerably at their anterior parts, while, during expiration, they are relaxed and are separated from each other. Hence, the inspiration, especially in young individuals whose glottis respiratoria is narrow, is difficult and noisy (*Legallois*) ; while the expiration takes place easily. After a few days, the animal (carnivore) becomes more quiet, it respires with less effort, and the passive vibratory movements of the vocal cords become less. Even after a considerable interval, if the animal be excited, it is attacked with severe dyspnœa, which disappears only when the animal has become quiet again. Owing to paralysis of the laryngeal muscles, foreign bodies are apt to enter the trachea, while the paralysis renders difficult the first part of the process of swallowing in the œsophageal region. Broncho-pneumonia may be produced. [Effect of ether, see p. 663.]

2, pharyngeal branches of vagus ; 6, pharyngeal branch of the glosso-pharyngeal ; 3, superior laryngeal, with its anastomoses, *f*, with the sympathetic and its division, 4, into its internal, *v*, and external branches, *c* ; 5, inferior or recurrent laryngeal ; *au.*, auricular branch of vagus. *Cardiac nerves :—g*, cardiac branches from the vagus and superior laryngeal ; *i*, *h*, the three cardiac branches from the upper, *g*, middle, *x*, and lower, *y*, cervical ganglion of the sympathetic ; *k*, ring of Vieussens ; *l*, cardiac branch from the recurrent laryngeal ; *L*, lung with the anterior and posterior pulmonary plexuses ; *r*, œsophageal plexus ; *oo*, gastric branches, and near them the hepatic branches, *n* ; *m*, cœliac plexus ; *k*, splanchnic entering former ; 11, accessory nerve sending its inner branch into the gangliform plexus of the vagus—its outer branch, *ac*, supplies the sternomastoid, *St* and ac_1, and the trapezius, *Cc* ; *O*, external auditory meatus ; *Oh*, hyoid bone ; *K*, thyroid cartilage ; *T*, trachea ; *H*, heart ; *P*, pulmonary artery ; *A A*, aorta ; *c*, right carotid ; c_1, left carotid ; *s* and s_1, right and left subclavian artery ; *Z Z*, diaphragm ; *N*, kidney ; *Nn*, suprarenal capsule ; *M*, stomach ; *m*, spleen ; *L L*, lung and liver. II. *Scheme of the course of the depressor and accelerans in the cat.*

6. The **depressor nerve**, which in the rabbit arises by one branch from the superior laryngeal, and usually also by a second root from the trunk of the vagus itself [runs down the neck in close relation with the vagus, sympathetic, and carotid artery, enters the thorax], and joins the cardiac plexus (fig. 524, *sc*). It is an **afferent nerve**, and when its *central* end is stimulated [provided both vagi be divided], it diminishes the energy of the vaso-motor centre, and thus causes a fall of the blood-pressure (hence the name given to it by Cyon and Ludwig, § 371, II.). At the same time, [if the vagus on the opposite side be intact], its stimulation affects the *cardio-inhibitory centre*, and thus reflexly diminishes the number of heart-beats. [Its stimulation also gives rise to **pain**, so that it is the sensory nerve of the heart. If in a rabbit the vagi be divided in the middle of the neck, and the **central** end of the depressor nerve, which is the smallest of the three nerves near the carotid, be stimulated, after a short time there is no alteration of the heart-beats, but there is steady fall of the blood-pressure (fig. 119), which is due to a reflex inhibition of the vaso-motor centre, resulting in a dilatation of the blood-vessels of the abdomen. Of course, if the vagi be intact, there is a reflex inhibitory effect on the heart. It is doubtful if the depressor comes into action when the heart is over-distended. If it did, of course the blood-pressure would be reduced by the reflex dilatation of the abdominal blood-vessels.]

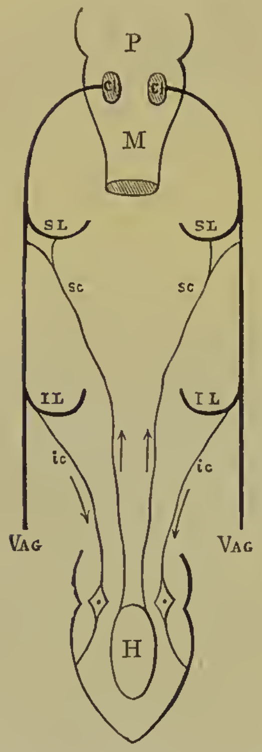


Fig. 524.
Scheme of the cardiac nerves in the rabbit. P, pons; M, medulla oblongata; VAG, vagus; SL, superior, IL, inferior laryngeal; *sc*, superior cardiac or depressor; *ic*, inferior cardiac or cardio-inhibitory; H, heart.

The depressor nerve is present in the cat (§ 370), hedgehog (*Aubert, Röver*), rat and mouse; in the horse and in man, fibres analogous to the depressor re-enter the trunk of the vagus (*Bernhardt, Kreidmann*). Depressor fibres are also found in the rabbit in the trunk of the vagus (*Dreschfeldt, Stelling*).

7. The **cardiac branches** (fig. 523, *g*, *l*), as well as the cardiac plexus, have been described in § 57. These nerves contain the **inhibitory fibres for the heart** (fig. 524, *ic*—**cardio-inhibitory**—*Edward Weber*, November, 1845; *Budge*, independently in May 1846), also **sensory fibres** for the heart [in the frog (*Budge*), and partly in mammals (*Goltz*)]. Lastly, in some animals the heart receives some of the *accelerating* fibres through the trunk of the vagus. Feeble stimulation of the vagus occasionally causes acceleration of the beats of the heart (*Schiff*). [This occurs when the vagus contains accelerator fibres.] In an animal poisoned with nicotin, or atropin, which paralyses the inhibitory fibres of the vagus, stimulation of the vagus is followed by acceleration of the heart-beats (*Schiff*, *Schmiedeberg*) [owing to the unopposed action of any accelerated fibres that may be present in the nerve, *e.g.*, of the frog].

8. The **pulmonary branches** of the vagus join the anterior and posterior pulmonary plexuses. The **anterior pulmonary plexus** gives **sensory** and **motor** fibres to the trachea, and runs on the anterior surface of the branches of the bronchi into the lungs (*L*). The **posterior plexus** is formed by three to five large branches from the vagus, near the bifurcation of the trachea, together with branches from the lowest cervical ganglion of the sympathetic and fibres from the cardiac plexus. [It also receives fibres from the second, third, and fourth thoracic ganglia of the sympathetic; and through the latter channels the vaso-constrictor fibres reach the blood-vessels of the lung (§ 371).] The plexuses of opposite sides exchange fibres, and branches are given off which accompany the bronchi in the lungs.

Ganglia occur in the course of the pulmonary branches in the frog (*Arnold*, *W. Stirling*) [newt—*W. Stirling;* and in mammals (*Remak*, *Egorow*, *W. Stirling*)], in the larynx [*Cock*, *W. Stirling*], in the trachea and bronchi [*W. Stirling*, *Kandarazki*]. Branches proceed from the pulmonary plexus to the pericardium and the superior vena cava (*Luschka*, *Zuckerkandl*).

The **functions** of the **pulmonary branches of the vagus** are—(1) they supply **motor branches** to the smooth muscles of the whole bronchial system (§ 106); (2) they supply a small part of the **vaso-motor nerves** of the pulmonary vessels (?) (*Schiff*), but by far the largest number of these nerves (? all) is supplied from the connection with the sympathetic (in animals from the upper dorsal ganglion)—(*Rose and Bradford*, § 371, *A. Fick*, *Badoud*, *Lichtheim*); (3) they supply **sensory** (cough-exciting) fibres to the whole bronchial system, and to the lungs; (4) they give **afferent** fibres, which, when stimulated, diminish the activity of the *vaso-motor centre*, and thus cause a fall of the blood-pressure during forced expiration; (5) similar fibres which act upon the inhibitory centre of the heart, and so influence it as to accelerate the pulse-beats (§ 369, II.). Simultaneous stimulation of 4 and 5 alters the pulse rhythm (*Sommerbrodt*); (6) they also contain *afferent* fibres from the pulmonary parenchyma to the medulla oblongata, which *stimulate the respiratory centre.* [These fibres are continually in action], and consequently section of both vagi is followed by diminution of the number of respirations; the respirations become at the same time deeper, while the same volume of air is changed (*Valentin*). Stimulation of the *central* end of the vagus again accelerates the respirations (*Traube*, *J. Rosenthal*). Thus, laboured and difficult respiration is explained by the fact that the influences conveyed by these fibres which excite the respiratory centre reflexly are cut off; so it is evident that centripetal or afferent impulses proceeding upwards in the vagus are intimately concerned in maintaining normal reflex respiration; after these nerves are divided, conditions exciting the respiratory movements must originate *directly*, especially in the medulla oblongata itself (§ 368).

Pneumonia after Section of both Vagi.—The inflammation which follows section of both vagi has attracted the attention of many observers since the time of Valsalva, Morgagni (1740), and Legallois (1812). In attempting to explain this phenomenon, we must bear in mind the following considerations :—(a) Section of both vagi is followed by loss of *motor* power in the muscles of the larynx, as well as the *sensibility* of the larynx, trachea, bronchi, and the lungs, provided the section be made above the origin of the superior laryngeal nerves. Hence, the glottis is not closed during swallowing, nor is it closed reflexly when foreign bodies (saliva, particles of food, irrespirable gases) enter the respiratory passages. Even the reflex act of *coughing*, which, under ordinary circumstances, would get rid of the offending bodies, is abolished. Thus, foreign bodies may readily enter the lungs, and this is favoured by the fact that, owing to the simultaneous paralysis of the œsophagus, the food remains in the latter for a time, and may therefore easily enter the larynx. That this constitutes one important factor was proved by Traube, who found that the pneumonia was prevented when he caused the animals to respire by means of a tube inserted into the trachea through an aperture in the neck. If, on the contrary, only the motor recurrent nerves were divided and the œsophagus ligatured, so that in the process of attempting to swallow, food must necessarily enter the respiratory passages, "traumatic pneumonia" was the invariable result (*Traube*, *O. Frey*). (b) A second factor depends on the circumstance that, owing to the laboured and difficult respiration, the *lungs become surcharged with blood*, because during the long time that the thorax is distended, the pressure of the air within the lungs is abnormally low. This condition of congestion, or abnormal filling of the pulmonary vessels with blood, is followed by *serous exudation* (pulmonary œdema) and even by exudation of blood and the formation of pus in the air-vesicles (*Frey*). This same circumstance favours the entrance of fluids through the glottis (§ 352, *b*). The introduction of a trachea cannula will prevent the entrance of fluids and the occurrence of inflammation. It is probable that a partial *paralysis* of the *pulmonary vaso-motor* nerves may be concerned in the inflammation, as this conduces to an engorgement of the pulmonary capillaries. (c) Lastly, it is of consequence to determine whether *trophic* fibres are present in the vagus, which may influence the normal condition of the pulmonary tissues. According to Michaelson, the pneumonia which takes place *immediately* after section of the vagi occurs especially in the lower and middle lobes; the pneumonia which follows section of the recurrents occurs *more slowly*,

and causes catarrhal inflammation, especially in the upper lobes. Rabbits, as a rule, die within twenty-four hours, with all the symptoms of pneumonia; when the above-mentioned precautions are taken, they may live for several days. Dogs may live for a long time. If the 9th, 10th, and 12th nerves be torn out on one side in a rabbit, death takes place from pneumonia (*Grünhagen*). In **birds**, bilateral section of the vagi is not followed by pneumonia (*Blainville, Billroth*), because the upper larynx remains capable of closing firmly—death takes place in eight to ten days with the symptoms of *inanition* (*Einbrodt, Zander, v. Anrep*), while the **heart** undergoes **fatty degeneration** (*Eichhorst*), and so do the liver, stomach, and muscles (*v. Anrep*). According to Wassilieff, the heart shows cloudy swelling and slight wax-like degeneration. **Frogs**, which at every respiration open the glottis, and close it during the pause, die of asphyxia. Section of the pulmonary branches has no injurious effect (*Bidder*). [Unilateral section of the vagus in **rabbits** is followed within forty-eight hours by the appearance of yellowish-white spots on the myocardium, especially near the interventricular septum, on the papillary muscles, and along the furrows for the coronary arteries. The muscular fibres exhibit retrogressive changes, whereby their striæ disappear; they become swollen up and filled with albuminous granules. After eight to ten days, the interstitial tissue of these foci becomes infiltrated with small round granular cells, especially near the blood-vessels. At a later stage the interstitial connective-tissue increases in amount, and the muscle atrophies. No effect is produced by section of the depressor or sympathetic, and Fantino concludes that some of the fibres of the vagus exert a trophic action on the myocardium.]

9. The **œsophageal plexus** (fig. 524, *r*) is formed principally by branches from the vagus above the inferior laryngeal, from the pulmonary plexus, and below from the trunk itself. This plexus supplies the œsophagus with **motor** power (§ 156), the **sensibility** which is present only in the upper part, and it also supplies fibres capable of exciting *reflex* actions.

10. The **gastric plexus** (*oo*) consists of (*a*) the anterior (left) termination of the vagus, which supplies fibres to the œsophagus and courses along the small curvature, and sends a few fibres through the portal fissure into the liver; (*b*) the posterior (right) vagus, after giving off a few fibres to the œsophagus, takes part in the formation of the gastric plexus to which (*c*) *sympathetic* fibres are added at the pylorus. *Section of the vagi* is followed by hyperæmia of the gastric mucous membrane (*Panum, Pincus*), but it does not interfere with digestion (*Bidder and Schmidt*), even when it is performed at the cardia (*Kritzler, Schiff*).

After bilateral section of the vagi below the diaphragm, the animal loses flesh, and after three months or so there are inflammatory changes in the gastric mucous membrane and pericellular proliferation in the liver and kidneys, and ultimately death takes place.

11. About two-thirds of the *right* vagus on the stomach joins the **cœliac plexus** (*m*) and from it branches accompany the arteries to the liver, spleen, pancreas, duodenum, kidneys, and suprarenal capsules. The vagus supplies **motor fibres** to the stomach, which belong to the root of the vagus itself and not to the accessorius (*Stilling, Bischoff*). The gastric branches also contain *afferent* fibres, which, when stimulated, cause *reflexly a secretion of saliva* (§ 145). It is undetermined whether they also cause vomiting. (For the effect of the **vagus** upon the **movements of the intestine** see § 161). According to some observers, stimulation of the vagus is followed by movement of the large as well as of the small intestine (*Stilling, Kupffer, C. Ludwig, Remak*). Stimulation of the *peripheral* end of the vagus causes contraction of the smooth muscular fibres in the capsulæ and trabeculæ of the *spleen* (in the rabbit and dog, § 103). Stimulation of the vagus at the cardia causes increase in the secretion of urine with dilatation of the *renal vessels*, while the blood of the renal vein becomes more arterial (*Cl. Bernard*). According to Rossbach and Quellhorst, a few *vaso-motor* fibres are supplied by the vagus to the abdominal organs, whilst the greatest number comes from the splanchnic.

12. **Reflex Effects discharged from the Vagus.**—The vagus and its branches contain fibres, some of which have been referred to already, which act *reflexly* (afferent) *upon certain nervous mechanisms.*

(*a*) On the **vaso-motor centre** there act (*α*) **pressor fibres** (especially in both laryngeal nerves) whose stimulation is followed by a reflex contraction of the

arterial blood-channels, and thus cause a rise of the blood-pressure; (β) depressor fibres (in the depressor or the vagus itself), which have exactly an opposite effect. (This subject is specially referred to under the head of the *Vaso-motor nerve-centre*, § 371).

(*b*) On the **respiratory centre** there act (α) fibres (pulmonary branches) whose stimulation is followed by **acceleration** of the respiration; and (β) **inhibitory fibres** (in both laryngeals), whose stimulation is followed by slowing or arrest of the respiration. (See *Respiratory centre*, § 368.)

(*c*) On the **cardio-inhibitory system.**—[When the *central* end of one vagus is stimulated, provided the other vagus is intact, the heart may be arrested *reflexly* in the diastolic phase.] Mayer and Pribram observed that sudden distention of the stomach caused slowing and even arrest of the heart, while, at the same time, there was contraction of the arteries of the medulla oblongata and increase of the blood-pressure.

(*d*) On the **vomiting centre.**—This centre may be affected by stimulation of the *central* end of the vagus, and, as already mentioned, by stimulation of many afferent fibres in the vagus (§ 158).

(*e*) On the **pancreatic secretion.**—Stimulation of the *central* end of the vagus is followed by arrest of this secretion (§ 171).

(*f*) According to Cl. Bernard, there are fibres present in the pulmonary nerves, which, when they are stimulated, increase reflexly the **formation of sugar in the liver**, perhaps through the hepatic branches of the vagus.

Unequal Excitability of the branches of the vagus.—The various branches of the vagus are not all endowed with the same degree of *excitability*. If the *peripheral* end of the vagus be stimulated first of all with a weak stimulus, the laryngeal muscles are first affected, and afterwards the heart is slowed (*Rutherford*). If the *central* end be stimulated with feeble stimuli, the "excito-respiratory" fibres are exhausted before the "inhibito-respiratory" (*Burkart*). According to Steiner, the various fibres are so arranged in the vagus that the afferent fibres lie in the outer, and the efferent in the inner, half of the trunk, in the cervical region.

Pathological.—Stimulation or paralysis in the area of the vagus must necessarily present a very different picture according as the affection is referred to the whole trunk or only to some of its branches, or whether the affection is unilateral or bilateral. **Paralysis of the pharynx and œsophagus**, which is usually of central or intracranial origin, interferes with or abolishes deglutition, so that when the œsophagus becomes filled with food there is difficulty of breathing, and the food may even pass into the nasal cavities. A peculiar sonorous gurgling is occasionally heard in the relaxed canal (deglutatio sonora). In **incomplete paralysis**, the act of deglutition is delayed and rendered more difficult, while large masses are swallowed more easily than small ones. *Increased contraction* and spasmodic stricture of the œsophagus are referred to under the phenomena of general nervous excitability (§ 186).

Spasm of the laryngeal muscles causes spasmodic closure of the glottis (*Spasmus glottidis*). This condition is most apt to occur in children, and takes place in paroxysms, with symptoms of dyspnœa and crowing inspiration; if the case be very severe, there may be muscular contractions (of the eye, jaw, digits, &c.). The symptoms are very probably due to the reflex spasms which may be discharged from the sensory nerves of several areas (teeth, intestine, skin). The impulse is conducted along the sensory nerves proceeding from these areas to the medulla oblongata, where it causes the discharge of the reflex mechanism which produces the above-mentioned results. There may be spasm of the dilators of the glottis and other laryngeal muscles (*Fräntzel*).

Stimulation of the **sensory nerves** of the larynx, as is well known, produces coughing. If the stimulation be very intense as in whooping-cough, the fibres lying in the laryngeal nerves, which *inhibit* the respiratory centre, may also be stimulated; the number of respirations is diminished, and ultimately the respiration ceases, the diaphragm being relaxed; while, with the most intense stimulation, there may be spasmodic expiratory arrest of the respiration with closure of the glottis, which may last for fifteen seconds. *Paralysis of the laryngeal nerves*, which causes disturbances of *speech*, has been referred to in § 313. In *bilateral paralysis of the recurrent nerves*, in consequence of tension upon them due to dilatation of the aorta and the subclavian artery, a considerable amount of air is breathed out, owing to the futile efforts which the patient makes in trying to speak; expectoration is more difficult, while violent coughing is impossible (*v. Ziemssen*). Attacks of dyspnœa occur just as in animals, if the person makes violent efforts. Some observers (*Salter*, *Bergson*) have referred the paroxysms of nervous asthma, which last for a quarter of an hour or more, and constitute *asthma bronchiale*, to stimulation of the pulmonary plexus, causing spasmodic contraction of the bronchial muscle (§ 106). Physical investigation during the paroxysms reveals nothing but the existence of some

rhonchi (§ 117). If this condition is really spasmodic in its nature (? of the vessels), it must be usually of a reflex character; the afferent nerves may be those of the lung, skin, or genitals (in hysteria). Perhaps, however, it is due to a temporary paralysis of the pulmonary nerves (afferent), which excite the respiratory centre (excito-respiratory).

Stimulation of the **cardiac** branches of the vagus may cause attacks of temporary suspension of the cardiac contractions, which are accompanied by a feeling of great depression and of impending dissolution, with occasionally pain in the region of the heart. Attacks of this sort may be produced *reflexly*, *e.g.*, by stimulation or irritation of the abdominal organs (as in the experiment of Goltz of tapping the intestines, § 369, II.). Hennoch and Silbermann observed slowing of the action of the heart in children suffering from gastric irritation. Similarly, the respiration may be affected reflexly through the vagus, a condition described by Hennoch as **asthma dyspepticum.** In cases of intermittent paralysis of the cardiac branches of the vagus, we rarely find *acceleration* of the pulse above 160 (*Riegel*), 200 (*Tuczek*, *L. Langer*); even 240 pulse-beats per minute have been recorded (*Kuppert*), and in such cases the beats vary much in rhythm and force, and they are very irregular. These cases require to be more minutely analysed, as it is not clear how much is due to paralysis of the vagus and how much to the action of the accelerating mechanism of the heart. Little is known of affections of the *intra-abdominal* fibres of the vagus. It seems that the sensory branches of the stomach do not come from the vagus. If the trunk of the vagus or its centre be paralysed, there are laboured, deep, slow respirations, such as follow the section of both vagi (*Guttmann*).

353. XI. **NERVUS ACCESSORIUS WILLISII.**—Anatomical.—This nerve arises by two completely separate roots; *one* from the **accessorius** nucleus of the **medulla oblongata** (fig. 516, 11), which is connected with the vagus nucleus; while the *other* root arises between the anterior and posterior nerve-roots from the **spinal cord**, usually between the 5th and 6th cervical vertebræ (fig. 520). In the spinal cord its fibres can be traced to an elongated nucleus lying on the outer side of the anterior cornu, as far downwards as the 5th cervical vertebra. Near the jugular foramen both portions come together, but do not exchange fibres (*Holl*); both roots afterwards separate from each other to form two distinct branches, the **anterior** (*inner*), which arises from the medulla oblongata, passing *en masse* into the plexus gangliiformis vagi. This branch supplies the vagus with most of its **motor fibres** (compare § 352, 3), and also its **cardio-inhibitory fibres** (fig. 523). [The upper cervical metameres or segments give origin not only to the anterior and posterior roots of the corresponding nerve-roots, but *between* these roots arise the roots of the spinal accessory nerve. This nerve contains *large* medullated nerve-fibres, and *fine* medullated fibres such as characterise the visceral branches of the thoracic and sacral regions (§ 356). The nerve passes by the jugular ganglion of the vagus, then divides into the external and internal branch. All the **large fibres** pass into the external branch, which, along with branches from the cervical plexus, supply the sternomastoid and trapezius. The internal branch, composed of **small fibres**, passes into the ganglion of the trunk of the vagus. Gaskell therefore regards the internal branch "as formed by the rami viscerales of the upper cervical and vagus nerves." It has been suggested that these fine medullated nerve-fibres arise from the cells of the posterior vesicular column of Clarke. The motor fibres to the trapezius and sternomastoid arise from the cells of the lateral horn of grey matter.]

If the accessorius be pulled out by the root in animals, the cardio-inhibitory fibres undergo degeneration. If the trunk of the vagus be stimulated in the neck four to five days after the operation, the action of the heart is no longer arrested thereby [owing to the degeneration of the cardio-inhibitory fibres] (*Waller*, *Schiff*, *Daszkiewicz*, *Heidenhain*); according to Heidenhain, the heart-beats are accelerated immediately after pulling out the nerve.

The **external branch** arises from the spinal roots. This nerve communicates with the **sensory** branches of the posterior root of the 1st, more rarely of the 2nd cervical nerve, and these fibres supply sensibility to the muscles; it then turns backwards above the transverse process of the atlas, and terminates as a **motor** nerve in the sternomastoid and trapezius (fig. 523). The latter muscle usually receives motor fibres also from the cervical plexus (fig. 518).

The external branch communicates with several cervical nerves. These fibres either participate in the innervation of the above-named muscles, or the accessorius returns part of the sensory fibres supplied by the posterior roots of the two upper cervical nerves.

Pathological.—Stimulation of the *outer* branch causes tonic or clonic spasm of the above-named muscles, usually on one side. If the branch to the sternomastoid be affected alone, the head is moved with each clonic spasm. If the affection be bilateral, the spasm usually takes place on opposite sides alternately, while it is rare to have it on both sides simultaneously. In **spasm of the trapezius** the head is drawn backwards and to the side. *Tonic* contraction of the

flexors of the head causes the characteristic position of the head known as caput obstipum (spasticum) or **wryneck**. In *paralysis* of one of these muscles, the head is drawn towards the sound side (**torticollis paralyticus**). Paralysis of the trapezius is usually only partial.

Paralysis of the whole trunk of the spinal accessory (usually caused by central conditions), besides causing paralysis of the sternomastoid and trapezius, also paralyses the motor branches of the vagus already referred to (*Erb, Fränkel*).

354. **XII. NERVUS HYPOGLOSSUS.—Anatomical.**—It arises from two *large-celled* nuclei within the lowest part of the calamus scriptorius, and one adjoining *small-celled* nucleus (*Roller*), while additional fibres come from the brain (§ 378), and also perhaps from the olive (fig. 516, 12, 520). It springs by 10 to 15 twigs in a line with the anterior roots of the spinal nerve (fig. 516, IX.). In its development part of the hypoglossal behaves as a spinal nerve (*Froriep*).

Function.—It is **motor** to all the muscles of the **tongue**, including the geniohyoid and thyrohyoid.

Connections.—The trunk of the hypoglossal is connected with—(1) the *superior cervical ganglion* of the *sympathetic*, which supplies it with *vaso-motor* fibres for the blood-vessels of the tongue. After section of the hypoglossal and lingual nerves, the corresponding half of the tongue becomes red and congested (*Schiff*). (2) There is also a branch from the plexus gangliiformis vagi, its small lingual branch to the commencement of the hypoglossal arch. These fibres supply the hypoglossal with *sensory* fibres for the *muscles of the tongue*, for even after section of the lingual the tongue still possesses dull sensibility. It is uncertain whether fibres with a similar function are partly derived from the cervical nerves or from the anastomosis which takes place with the lingual. (3) It is united with the *upper cervical nerves* by means of the loops known as the ansa hypoglossi. These connecting fibres run in the descendens noni to the sternohyoid, omohyoid, and sternothyroid. Cervical fibres do not, as a rule, enter the tongue; stimulation of the root of the hypoglossal acts upon the above-named muscles only very rarely and to a very slight extent (*Volkmann*). [Beevor and Horsley find that the motor fibres which pass *viâ* the hypoglossal to innervate the muscles that depress the hyoid bone, are derived from the first and second cervical nerves.] (Compare § 297, 3, and § 336, III.).

Bilateral section of the nerve causes complete motor paralysis of the tongue. Dogs can no longer lap, they bite the flaccid tongue. Frogs, which seize their prey with the tongue, must starve; when the tongue hangs from the mouth, it must prevent the closure of the mouth, so that these animals must die from asphyxia, as air is pumped into the lungs only when the mouth is closed.

Pathological.—Paralysis of the hypoglossal (**glossoplegia**), which is usually central in its origin, causes disturbance of *speech* (§ 319). [In unilateral palsy, the tongue lies in the mouth in its normal position, but the base is more prominent on the paralysed side. When the tongue is protruded, it passes to the sound side by the genio-hyoglossus (§ 155).] Paralysis of the tongue also interferes with mastication, the formation of the bolus in the mouth, and deglutition in the mouth. Owing to the imperfect movements of the tongue, *taste* is imperfect, and the singing of high notes and the falsetto voice, which require certain positions of the tongue, appear to be impossible (*Bennati*).

Spasm of the tongue, which causes aphthongia (§ 318), is usually reflex in its origin, and is extremely rare. Idiopathic cases of spasm of the tongue have been described; the seat of the irritation lay either in the cortex cerebri or in the oblongata (*Berger, E. Remak*). For **Pseudo-motor Action**, § 349.

355. **THE SPINAL NERVES.—Anatomical.**—The **thirty-one pairs** of spinal nerves arise by means of a [superior, gangliated] **posterior root** (consisting of a few large rounded bundles), from the sulcus between the posterior and lateral columns of the spinal cord, and by means of an [inferior, non-gangliated] **anterior root** (consisting of numerous fine flat strands), from the furrow between the anterior and lateral columns (fig. 525). The posterior roots, with the exception of the 1st cervical nerve, are the larger. Occasionally the roots on opposite sides are not symmetrical; one or other root, or even a whole nerve, may be absent from the dorsal region (*Adamkiewicz*). On the **posterior root** is the spindle-shaped **spinal ganglion** (§ 321, II., 3), which is occasionally double on the lumbar and sacral nerves. *Beyond the ganglion*, the two roots unite to form within the spinal canal the mixed trunk of a **spinal nerve.** The branches of the nerve-trunk invariably contain fibres coming from both roots. The number of fibres in the nerve-trunk is exactly the same as in the two roots; hence, we must conclude that

the nerve-cells in the spinal ganglion are intercalated in the course of the afferent fibres (*Gaule and Birge*).

Varieties.—The spinal ganglion is sometimes double, and according to Hyrtl, isolated ganglionic cells frequently occur in the posterior root, between the ganglion and the cord; [and they also occur in the anterior roots]. Occasionally the roots are somewhat unsymmetrical on opposite sides; in the dorsal part one or other, or both roots of a spinal nerve, are sometimes absent.

[**Morphology of the Spinal Nerves and Limb-Plexuses.**—A typical **segmental spinal nerve** (fig. 525) divides, after its formation, into three parts, a **dorsal** branch, or superior primary division, distributed to the back, a **somatic** branch, or inferior primary division, supplying the body-wall or limbs; and a **splanchnic** or **visceral** branch, or ramus communicans, connected with the sympathetic gangliated cord, and distributed to the large vessels and viscera. The somatic branch is the largest, and is generally, by human anatomists, spoken of as the "anterior primary division." In the thoracic and upper lumbar regions the distribution of this nerve is simple. It divides into an external (or lateral) branch, and an internal (or anterior) branch, which supply respectively the lateral and anterior portions of the thoracic and abdominal walls.]

[In the region of the neck, and in relation to the limbs, the arrangement of the somatic branches becomes complicated by the formation of the **plexuses**. In the embryo, however, the distribution of the nerves is simpler, and a comparison can be made both with the adult arrangement, and with the typical nerve as seen in the thoracic region. In the embryo, the neck as such does not exist, and the upper limb sprouts out directly beyond the segmented visceral arches. In this state the somatic branch is distributed as in the thoracic region; the nerve divides into an external and an internal branch, distributed to the side and front of the corresponding part of the arches in the neck, in the regions where the limbs are appearing as two flattened buds from the ventro-lateral aspect of the body. The somatic branch sweeps round into the blastema forming the limb, and divides into its two branches, external and internal, or dorsal and ventral, which are distributed to the outer (dorsal) and inner (ventral) surfaces, respectively, of the primitive limb. At this time the cartilaginous and muscular elements of the limb have not become differentiated. While this is occurring the dorsal and ventral parts of the somatic branches of the nerves entering the limb unite with adjacent dorsal and ventral branches, in various combinations, so as to produce the limb-plexuses. The nerves resulting from these combinations are distributed to the primitive, dorsal, and ventral surfaces of the limbs. Thus, the plexuses are formed, and the peripheral distribution of the nerves has taken place before the period of flexion and angulation of the limbs. These processes mark the conditions in the adult; but even then it is easy to make out that the nerves in the upper limb derived from the posterior (dorsal) cords of the brachial plexus supply the scapular region, extensor surface of the arm and fore-arm, and the back of the hand,—parts which are derived from the dorsal surface of the primitive limb; while the nerves produced from the anterior (ventral) cords supply the pectoral region, front of the arm, fore-arm, and hand,—parts representing the primitive ventral surface.]

Fig. 525.

Diagram of a spinal nerve; C, spinal cord; *pr*, *ar*, posterior and anterior roots; SPD, IPD, superior and inferior primary divisions; *d v*, dorsal and ventral branches; *sr*, sympathetic root (*Ross*).

[In the lower limb, the nerves derived from a union of the posterior branches are the external cutaneous, anterior crural, gluteal, and external popliteal. These supply the iliac surfaces, the front of the thigh, leg, and foot,—belonging to the primitive dorsal surface of the limb. The nerves formed by the union of anterior branches, genitocrural, obturator, and internal popliteal, in like manner supply the parts of the limb corresponding to the ventral surface,—the inner side and back of the thigh, the back of the leg, and the sole of the foot (*A. M. Paterson*).]

[**Structure of a Spinal Ganglion.**—The ganglion is invested by a thin, firmly adherent sheath of connective-tissue, which sends processes into the swelling, and

continuous with the sheaths of the nerve entering and leaving the ganglion (fig. 526, c). In **mammals**, *e.g.*, rabbit, a longitudinal section of such a ganglion exhibits the cells arranged in groups, with strands of nerve-fibres coursing longitudinally between them (fig. 526, a, b). The nerve-cells are usually globular in form, with a distinct capsule lined with epithelium, and the cell-substance itself contains a well-defined nucleus with a nuclear envelope and a nucleolus (fig. 527). The capsule of the cell is continuous with the sheath of Schwann of a nerve-fibre. The exact relation between the nerve-fibres and the nerve-cells is difficult to establish, but it is probable that each nerve-cell is connected with one nerve-fibre, *i.e.*, they are **unipolar.** In the spinal ganglia of the vertebrates above fishes, and also in the Gasserian ganglion, cells are found with a single process or fibre attached to them, the nerve-fibre process not unfrequently coiling a few times within the capsule. This process, after emerging from the capsule, becomes coated with myelin, and usually soon divides at a node of Ranvier (fig. 527, c). Ranvier, who first observed this arrangement, describes it as a T-shaped fibre. These nerve-cells with T-shaped fibres have been observed in the spinal ganglia of all vertebrates above fishes, in the Gasserian and geniculate ganglia, as well as in the jugular and cervical ganglia of the vagus. In **fishes**, the nerve-cells of the spinal ganglia are bipolar (fig. 446, 4). There is a rich plexus of capillaries in these ganglia, and each cell is surrounded by a meshwork of capillaries, which never penetrate the cell capsules.]

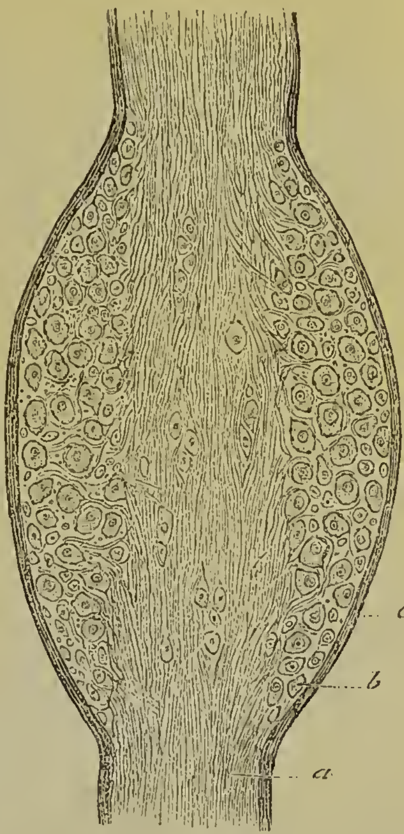


Fig. 526.
Longitudinal section of a spinal ganglion. a, nerve-fibre; b, nerve-cells; c, capsule.

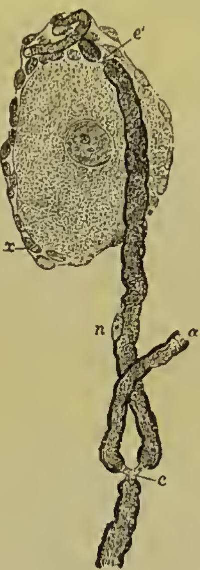


Fig. 527.
Nerve-cell isolated from the spinal ganglion, and showing a nerve-fibre divided in a T-shaped manner; x, nuclei of cells lining the cell-capsule; c', first, and c, second node of Ranvier; n, nucleus of nerve-fibre; a, nerve-fibre.

Bell's Law.—Sir Charles Bell discovered (1811) that the **anterior roots** of the spinal nerves are **motor**, the **posterior** are **sensory.**

Recurrent Sensibility.—Magendie discovered (1822) the remarkable fact that *sensory fibres* are *also present* in the anterior roots, so that their stimulation causes pain. This is due to the fact that sensory fibres pass into the anterior root after the two roots have joined, and these fibres run in the anterior root in a centripetal direction (*Schiff*, *Cl. Bernard*). The sensibility of the anterior root is abolished at once by section of the posterior root. This condition is called "recurrent sensibility" of the anterior root. When the sensibility of the anterior root is abolished, so is the sensibility of the surface of the spinal cord in the neighbourhood of the root. A long time after section of the anterior, and when the degeneration phenomena have had time to develop (§ 325), a few non-degenerated sensory fibres are always

to be found in the central stump (*Schiff, Vulpian*). Schiff found that in cases where the motor fibres had undergone degeneration, there were always non-degenerated fibres to be found in the anterior root, which passed into the membranes of the spinal cord. The sensory fibres pass into the motor root, either at the angle of union of the roots, or in the plexus, or in the region of the peripheral terminations. Sensory fibres enter many of the branches of the motor cranial nerves at their periphery, and afterwards run in a centripetal direction (p. 737). Even into the trunks of *sensory* nerves, sensory branches of other sensory nerves may enter. This explains the remarkable observation, that after section of a nerve trunk (*e.g.*, the median), its peripheral terminations still retain their sensibility (*Arloing and Tripier*). The tissue of the motor and sensory nerves, like most other tissues of the body, is provided with sensory nerves (*Nervi nervorum*, p. 654).

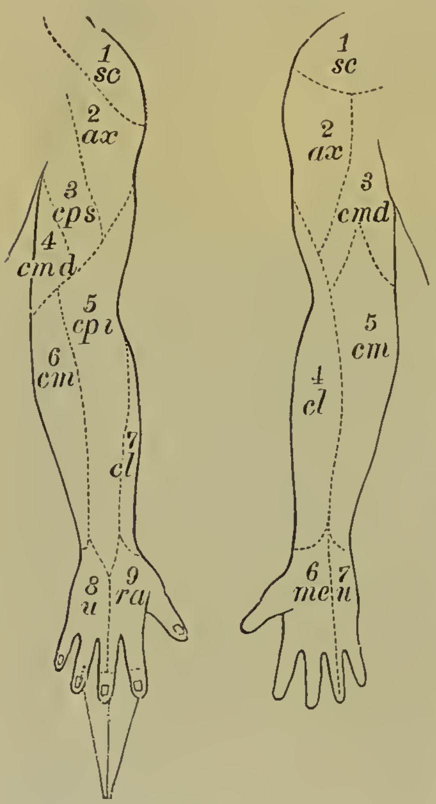


Fig. 528.

Distribution of the cutaneous nerves of the arm. A, Dorsal surface—*1 sc*, supra-clavicular ; *2 ax*, axillary ; *3 cps*, superior posterior cutaneous ; *4 cmd*, median cutaneous ; *5 cpi*, inferior posterior cutaneous ; *6 cm*, median cutaneous ; *7 cl*, lateral cutaneous ; 8 *u*, ulnar ; *9 ra*, radial ; *10 me*, median. B, volar surface—*1 sc*, supra-clavicular ; *2 ax*, axillary ; *3 cmd*, internal cutaueous ; *4 cl*, lateral cutaneous ; *5 cm*, cutaneous medius ; *6 me*, median ; *7 u*, ulnar.

[It does not follow that section of a peripheral cutaneous nerve will cause anæsthesia in the part to which it is distributed ; in fact, one of the principal nerve trunks of the brachial plexus may be divided without giving rise to complete anæsthesia in any part of the area of distribution of the sensory branches of the nerve, and even if there be partial or complete cutaneous anæsthesia, it is much less iu extent than corresponds to the anatomical area of distribution. The anæsthetic area tends to become smaller in extent (*Ross*). Thus, there is not complete independence in the distributiou of these nerves. These results are explained by the anastomosis between branches of nerves, the exchange of fibres in the terminal networks, while some sensory fibres enter the peripheral parts of a nerve aud run centripetally, perhaps being distributed to the skin and conferring recurrent sensibility on the peripheral part of the nerve.]

Deduction from Bell's Law.—Careful observations of the effects of section of the roots of the spinal nerves (*Magendie*, 1822), as well as the discovery of the reflex relation of the stimulation of the sensory roots to the anterior, constituting reflex movements (*Marshall Hall, Johannes Müller*, 1832), enable us to deduce the following conclusions from Bell's law :—1. At the moment of section of the **anterior root** there is a *contraction* in the muscles supplied by this root. 2. There is at the same time a *sensation of pain* due to the "recurrent sensibility." 3. After the section, the corresponding *muscles* are *paralysed*. 4. Stimulation of the peripheral trunk of the anterior root (immediately after the operation) causes *contraction* of the muscles, and eventually pain, owing to the recurrent sensibility. 5. Stimulation of the central end is *without effect*. 6. The sensibility of the paralysed parts is retained completely. At the moment of section of the **posterior root**, there is severe *pain*. 8. At the same time movements are discharged reflexly. 9. After the section, all parts supplied by the divided roots are devoid of sensibility. 10. Stimulation of the peripheral trunk of the divided nerve is without effect. 11.

Stimulation of the central end causes *pain* and *reflex* movements. 12. The central end ultimately degenerates. 13. Movement is retained completely in the paralysed parts, *e.g.*, in the extremities.

The **ultimate effects**, known as Wallerian degeneration, which follow section of the nerve or its roots, are referred to in § 325. Recently, Joseph has slightly modified the statements of Waller on the degeneration in the posterior roots. According to him, the spinal ganglion is the nutritive centre for by far the largest number of the fibres of this root; but individual fibres traverse the ganglion without forming connections with its cells, so that the nutritive or trophic centre for this small number of nerve-fibres is in the spinal cord.

Inco-ordinated Movements of Insensible Limbs.—After section of the posterior roots, *e.g.*, of the nerves for the posterior extremities, the muscles retain their movements, nevertheless there are characteristic disturbances of their motor power. This is expressed in the awkward manner in which the animal executes its movement—it has lost to a large extent its harmony and elegance of motion. This is due to the fact that, owing to the absence of the sensibility of the muscles and skin, the animal is no longer conscious of the resistance which is opposed to its movements. Hence, the degree of muscular energy necessary for any particular effort cannot be accurately graduated. Animals which have lost the sensibility of their extremities often allow their limbs to lie in abnormal positions, such as a healthy animal would not tolerate. In man also, when the peripheral ends of the cutaneous nerves are degenerated, there are **ataxic** phenomena (§ 364, 3).

Increased Excitability.—Harless (1858), Ludwig, and Cyon (controverted by v. Bezold, Uspensky, Grünhagen, and G. Heidenhain) observed that the anterior roots are more excitable as long as the posterior roots remain intact and are sensitive, and that their excitability is diminished as soon as the posterior roots are divided. In order to explain this phenomenon, we must assume that, in the intact body, a series of gentle impulses (impressions of touch, temperature, position of limbs, &c.) are continuously streaming through the posterior roots to the spinal cord, where they are transferred to the motor roots, so that a less stimulus is required to excite the anterior roots than when these reflex impulses of the posterior root, which increase the excitability, are absent. Clearly, a less stimulus will be required to excite a nerve already in a gentle state of excitement than in the case of a fibre which is not so excited. In the former case, the discharging stimulus becomes as it were superposed on the excitement already present. (Compare § 362.)

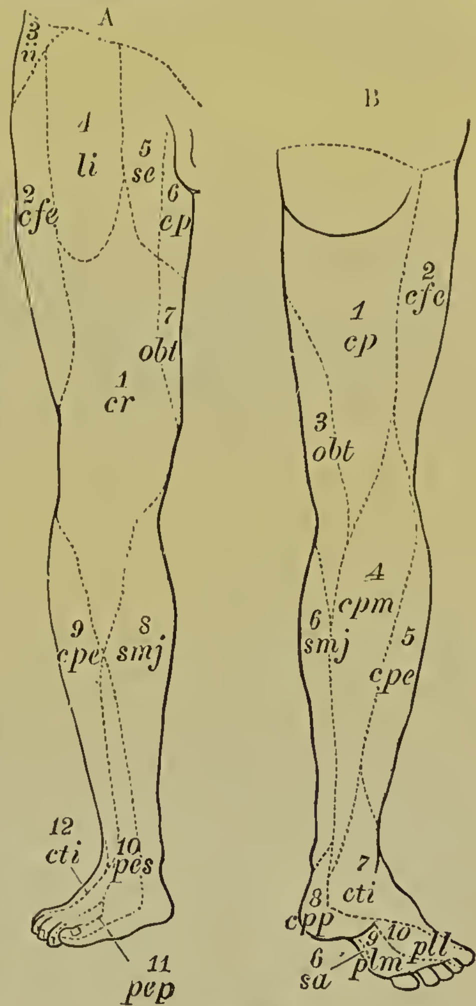


Fig. 529.

Distribution of the cutaneous nerves of the leg (after *Henle*). A, Anterior surface—1, crural nerve ; 2, external lateral cutaneous; 3, ilio-inguinal ; 4, lumbo-inguinal ; 5, external-spermatic ; 6, posterior cutaneous ; 7, obturator ; 8, great saphenous; 9, communicating peroneal ; 10, superficial peroneal; 11, deep peroneal; 12, communicating tibial. B, Posterior surface—1, posterior cutaneous ; 2, external femoral cutaneous ; 3, obturator ; 4, median posterior femoral cutaneous ; 5, communicating peroneal; 6, great saphenous ; 7, communicating tibial ; 8, plantar cutaneous ; 9, median plantar ; 10, lateral plantar.

The **anterior roots** of the spinal nerves supply **efferent fibres** to—

1. All the **voluntary muscles** of the trunk and extremities.

Every muscle always receives its motor fibres from *several* anterior roots (not from a single nerve-root). Hence, *every* root supplies branches to a particular group of muscles (*Prayrer*,

P. Bert, Gad). The experiments of Ferrier and Yeo show that stimulation of each of the anterior roots in apes (brachial and lumbo-sacral plexuses) caused a complex co-ordinated movement. Section of one root did not cause complete paralysis of the muscles concerned in these co-ordinated movements, although the force of the movement was impaired. These experiments confirm the results of clinical observation on man. The fibres for groups of muscles of different functions (*e.g.*, for flexors, extensors) arise from special limited areas of the spinal cord. The cervical and lumbar enlargements of the spinal cord are great centres for highly co-ordinated muscular movements.

2. The anterior roots also supply **motor fibres** for a number of organs provided with smooth muscular fibres, *e.g.*, the bladder (§ 280), ureter, uterus. [These are the viscero-motor nerves of Gaskell, and from them come also viscero-inhibitory nerves.]

3. **Motor fibres** for the smooth muscular fibres of the **blood-vessels**, the *vaso-motor*, **vaso-constrictor**, or vaso-hypertonic nerves [also **accelerator** or augmentor nerves of the heart]. They run in the sympathetic for a part of their course (§ 371).

4. **Inhibitory fibres** for the blood-vessels. These are but imperfectly known. They are also called **vaso-dilator** or vaso-hypotonic nerves (§ 372). [The spinal cord also supplies **inhibitory** nerves for the heart, which leave the spinal axis in the vagus.]

5. **Secretory fibres** for the sweat-glands of the skin (§ 289). For a part of their course they run in the sympathetic.

6. **Trophic fibres** of the tissues (§ 342, I., *c*).

The **posterior roots** contain all the **sensory nerves** of the skin and the internal tissues, except the front part of the head, face, and the internal part of the head. They also contain the **tactile nerves** for the areas of the skin already mentioned. Stimuli which discharge *reflex movements* are conducted to the spinal cord through the posterior roots. The sensory fibres of a mixed nerve-trunk supply the cutaneous area, which is moved by those muscles (or which covers those muscles) to which the same branch supplies the motor fibres. The special distribution of the motor and sensory nerves of the body belongs to anatomy (figs. 518, 519, 528, 529).

[**Physiology of the Limb-Plexuses.**—The idea that the nerve-strands become rearranged in the limb-plexuses so as to connect nerves derived from different parts of the spinal cord with particular groups of muscles, in order to allow of "co-ordination of muscular action," does not seem to be borne out by more extended observation. Herringham has shown by dissection (and the same is seen in cases of paralysis of motion and sensation) that a given muscle or part of a muscle, and a given spot of skin, are supplied by particular branches of individual spinal nerves proceeding directly from the spinal cord. The reason that the plexuses exist is, apparently, not a physiological one. Co-ordination cannot be effected in the plexus, where the axis-cylinder of the nerves do not divide; but only in the spinal cord and central nervous system, and through the intervention of nerve-cells. The existence of the plexuses is due to the fact that embryologically the limb consists of a flattened lappet, or bud, derived from certain somites, but at first presenting no signs of segmentation, with a preaxial and a postaxial border, and outer (dorsal) and inner (ventral) surfaces of skin, covering a double layer of muscle on each surface. The dorsal and ventral branches of the nerves supply these respective surfaces; and after the nerves have grown out, the simple muscular strata become split up into individual muscles, which contain elements derived from one or more segments represented in the primitive limb. Each nerve is segmental, and, therefore, supplies a muscle derived, for example, from the elements of two segments; the nerve of distribution must contain corresponding parts of two segmental nerves. The plexuses appear, therefore, from an embryological cause, and have no direct physiological significance (*A. M. Paterson*).]

356. THE SYMPATHETIC NERVE. — [Anatomical. — The sympathetic nervous system contains a large number of non-medullated or Remak's fibres, and consists of a series of **ganglia** lying on each side of the vertebral column and connected with each other by inter-ganglionic fibres. The typical distribution obtains in the thoracic region, where the **lateral** or vertebral ganglia lie close on the vertebræ. In front of this is a second series of ganglia, which do not form a double line, but are connected with the former and with each other. They are the pre-vertebral

or **collateral** ganglia, *e.g.*, semilunar, inferior mesenteric, &c., the nerves connecting them with the former being called rami efferentes. From these ganglia fibres proceed to connect them with ganglia lying in or about tissues or organs—the **terminal** ganglia (*Gaskell*).]

[Each spinal nerve in this region is connected with its corresponding sympathetic ganglion by the **ramus communicans,** which is formed by fibres both from the anterior and posterior roots of a spinal nerve. It corresponds to the visceral nerve of the morphologist, and is composed of two parts—a **white** and a **grey ramus.** The **white ramus** is composed entirely of **medullated** fibres, and coming from the anterior and posterior roots of a spinal nerve, passes into the lateral and collateral ganglia. These white rami occur in the dog only from the 2nd thoracic to the 2nd lumbar nerve (fig. 530). Above and below this the rami are all **grey** and composed of **non-medullated** nerve-fibres (*Gaskell*).]

[In **man**, the upper four rami communicantes from the four upper cervical nerves all join the superior cervical ganglion (fig. 517, *G g, s*), the 5th and 6th join the middle cervical, the 7th and 8th the inferior cervical ganglion. The lowest pair of ganglia are generally united by a loop on the front of the first coccygeal vertebra, and they lie in relation with the coccygeal ganglion.]

[**Cephalic Portion.**—As the sympathetic ascends to the head it forms connections with many of the cranial nerves, and there is a free exchange of fibres between these nerves. (The function and significance of these exchanges are referred to under the physiology of the cranial nerves).]

[**Dorsal and Abdominal Portion.**—Numerous fibres pass from these parts chiefly to the *thoracic* and *abdominal cavities,* where they form large gangliated plexuses, from which functionally different fibres proceed to the different organs.]

[In the **dog**, the 2nd, 3rd, 4th, and 5th thoracic pass upwards into the cervical sympathetic, those in the dorsal region being directed downwards from the lateral ganglia to form the **splanchnics** (fig. 530). The grey non-medullated nerve-fibres of each grey ramus are connected with the cells of its ganglion (lateral); the fibres do not go beyond the ganglion, but really run *to* the corresponding spinal nerve to ramify in the sheaths of the nerves, the connective-tissue on the vertebræ and the dura mater, and perhaps the other spinal membranes; so that, according to Gaskell, no non-medullated nerves leave the central nervous system by the spinal nerve-roots. Thus, the white rami communicantes alone constitute the rami viscerales of the morphologist, and all the visceral nerves passing out from the central nervous system into the sympathetic system pass out by them alone. All the nerves in the white ramus are of small calibre

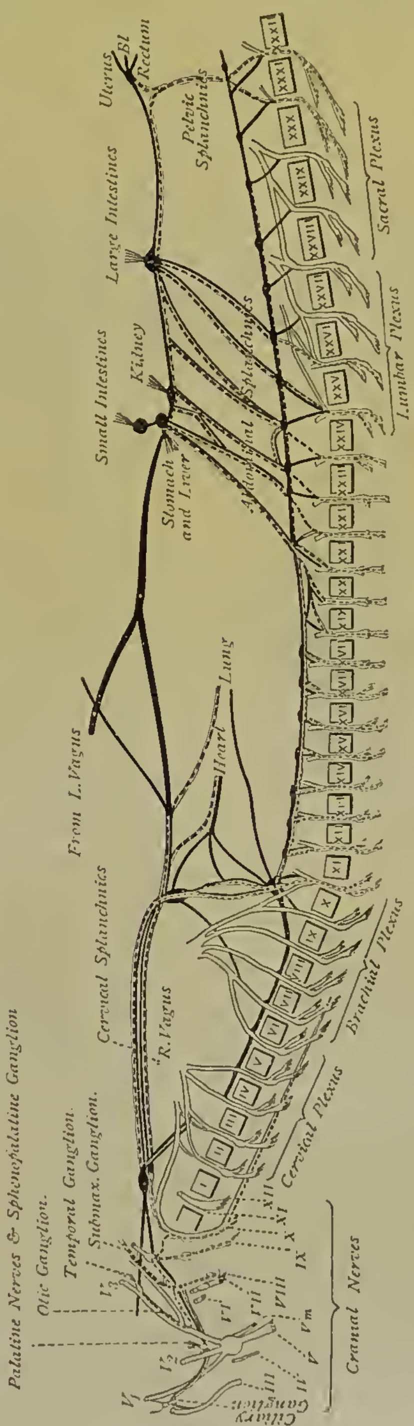


Fig. 530.

Diagram of the visceral nerves of the dog; the arrangement of the cranial visceral nerves is taken from Henle. The nerves which contain bundles of fine medullated nerve-fibres are indicated thus: - - - - -; those which consist chiefly of non-medullated fibres are indicated thus: ———. The formation of the rami viscerales in the cervico-cranial, thoracic, and sacral regions, and the general distribution of the visceral nerves are shown (*Gaskell*).

(1·8 μ to 2·7 μ) and medullated, while the true motor fibres are much larger (14·4 μ to 19 μ). The small, white fibres can be traced upwards as medullated fibres into the superior cervical ganglion, and in the thorax over the lateral ganglia to form the splanchnics into the collateral ganglia, beyond which they cease to be medullated. By the 2nd and 3rd sacral nerves some fibres of smallest calibre issue to form the **nervi erigentes**, which pass over and do not communicate with the lateral ganglia, but enter the hypogastric plexus, whence they send branches upwards to the inferior mesenteric plexus and downwards to the bladder, rectum, and generative organs. Gaskell proposes to call them the **pelvic splanchnic** nerves (fig. 530).]

[In the **cervical** region there is no white ramus, and the nerve-roots contain no nerve-fibres of small calibre. But in this region rises the **spinal accessory nerve**, between the anterior and posterior roots. It contains small and large nerve-fibres; the former pass into the internal division of this nerve and join the ganglion of the trunk of the vagus, while the large motor fibres form its external branch and supply the sternomastoid and trapezius muscles.]

[All the **vaso-motor nerves** arise in the central nervous system, and they leave the spinal cord as the finest medullated fibres in the anterior roots of all the spinal nerves between the 2nd thoracic and 2nd lumbar (dog) "along the corresponding ramus visceralis, enter the lateral or main sympathetic chain of ganglia, where they become non-medullated, and are thence distributed either directly or after communication with other ganglia" (*Gaskell*). In the lateral ganglia they terminate in the multipolar nerve-cells, where they become non-medullated; at least, this seems to be the case with some of the vaso-constrictor fibres.]

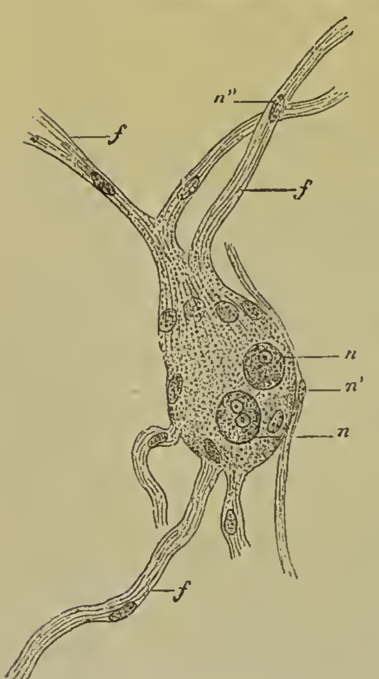


Fig. 531.
Nerve-cells isolated from the superior cervical sympathetic ganglion of a rabbit. *f f*, Remak's fibres; *n′n′*, nuclei of these fibres; *n n*, cell nuclei.

["The **vaso-dilator nerves** leave the central nervous system among the fine medullated fibres, which help to form the cervico-cranial and sacral rami viscerales, and pass without altering their character into the distal ganglia" (*Gaskell*).]

["The **viscero-motor nerves**, upon which the peristaltic contraction of the thoracic portion of the œsophagus, stomach, and intestines depends, leave the central nervous system in the out-flow of fine medullated nerves which occurs in the upper part of the cervical region, and pass by way of the rami viscerales, of the accessory and vagus nerves to the ganglion trunci vagi, where they become non-medullated" (*Gaskell*).]

["The **inhibitory nerves** of the circular muscles of the alimentary canal and its appendages leave the central nervous system in the anterior roots, and pass out among the fine medullated fibres of the rami viscerales into the distal ganglia without communication with the proximal ganglia" (*Gaskell*).]

[**Structure of a sympathetic ganglion.**—The structure of the sympathetic nerve-fibres and nerve-cells has already been described in § 321. On making a section of a **sympathetic ganglion**, *e.g.*, the human superior cervical, we observe groups of cells with bundles of nerve-fibres—chiefly non-medullated—running between them, and the whole surrounded by a laminated capsule of connective-tissue, which sends septa into the ganglion. The **nerve-cells** have many processes, and are, therefore, **multipolar**, and each cell is surrounded by a capsule with nuclei on its inner surface (fig. 446, II). The processes pierce the capsule, and one of them certainly—and perhaps all the processes—are connected with a nerve-fibre. Ranvier states that each cell has a fibrillated outer portion and a more granular inner part. Each of the processes becomes continuous with a fibre of Remak (fig. 531). Not unfrequently yellowish-brown pigment is found in the cell-substance. Similar cells have been

found in the ophthalmic, sub-maxillary, otic, and spheno-palatine ganglia. The number of medullated nerve-fibres diminishes as the sympathetic nerves are traced towards their distribution. Ranvier states that it is possible in the rabbit to trace the conversion of a medullated fibre into a branched fibre of Remak. The **blood-vessels** of the sympathetic ganglia in mammals are peculiar. The arteries are small, and after subdivision form a capillary network, each mesh of which encloses several ganglionic cells. The veins on the contrary are very large, tortuous, varicose, and often terminate in culs-de-sac, into which several capillaries open. The arrangement of the veins is spoken of as the **venous sinuses** of these ganglia, being compared by Ranvier to the sinuses of the dura mater and venous plexuses of the spinal canal.]

Functions of the sympathetic nerves. — The following is merely a *general* summary :—

I. Independent Functions of the sympathetic are those of certain nerve-plexuses which remain after all the nervous connections with the cerebro-spinal branches have been divided. The activities of these plexuses may be influenced—either in the direction of inhibition or stimulation—through fibres reaching them from the cerebro-spinal nerves.

To these belong :—

1. The automatic ganglia of the heart (§ 58).
2. The mesenteric plexus of the intestine (§ 161).
3. The plexuses of the uterus, Fallopian tubes, ureters (also of the blood- and lymph-vessels).

II. Dependent Functions.—Fibres run in the sympathetic, which (like the peripheral nerves) are active only when their connection with the central nervous system is maintained, *e.g.*, the sensory fibres of the splanchnic. Others again convey impulses from the central nervous system to the *ganglia*, while the ganglia in turn modify the impulses which inhibit or excite the movements of the corresponding organs.

The following statement is a *resumé* of the functions of the sympathetic, according to the anatomical arrangement :—

A. Cervical Part of the Sympathetic.

1. **Pupil-dilating fibres** (compare *Ciliary ganglion*, § 347, I., and *Iris*, § 392). According to Budge, these fibres arise from the spinal cord, and run through the upper two dorsal and lowest two cervical nerves into the cervical sympathetic, which conveys them to the head. Section of the cervical sympathetic or its rami communicantes causes contraction of the pupil. (The central origin of these fibres is referred to in § 362, 1, and § 367, 8.)

2. **Motor fibres** for Müller's smooth muscle of the orbit, and *partly* for the external rectus muscle (§ 348).

3. **Vaso-motor** branches for the outer ear and the side of the face (*Cl. Bernard*), tympanum (*Prussak*), conjunctiva, iris, choroid, retina (*only in part—see Ciliary ganglion*, § 347, I.), for the vessels of the œsophagus, larynx, thyroid gland—fibres for the vessels of the brain and its membranes (*Donders and Callenfels*). [In the dog the vaso-motor fibres for the head leave the cord by the anterior roots of the second, third, fourth, and fifth dorsal nerves, enter the corresponding sympathetic ganglia, and run through the annulus of Vieussens forwards into the cervical sympathetic, and thus reach their terminations in the blood-vessels of the head.]

4. In the cervical portion are afferent fibres which excite the vaso-motor centre in the medulla (*Aubert*).

5. **Secretory** (trophic) and **vaso-motor** fibres for the salivary glands (§ 145).

6. **Sweat-secretory** fibres (see § 288, II.).

7. According to Wolferz and Demtschenko the lachrymal glands receive sympathetic **secretory** fibres (?).

[The cervical sympathetic contains secretory fibres for the glands in the muzzle of the ox, but it also, according to Arloing, contains inhibitory-secretory fibres. It also seems to contain trophic nerve-fibres; at least marked histological changes occur in the muzzle of the ox and nose of the dog after section of the cervical sympathetic. In the dog, after two months or so, the skin of the nose becomes papillated and dry, while there is a great hypertrophy of the corneous layer of the epidermis.]

[**Section of the Cervical Sympathetic.**—This experiment is easily done on a rabbit, preferably an albino one. Divide the nerve in the neck, and immediately thereafter (1) the ear and adjoining parts on that side become greatly congested with blood, blood-vessels appear that were formerly not visible, and as a result of the increased quantity of blood in the ear (hyperæmia), there is (2) a rise of the temperature amounting to even 4° to 6° C. (*Cl. Bernard*). These are the *vaso-motor* changes. (3) The pupil is contracted, the cornea flattened, and there is retraction of the eyeball and consequent narrowing of the palpebral fissure. These are the *oculo-pupillary* symptoms. **Stimulation** (electrical) of the peripheral end produces the opposite results,—pallor of the ears, owing to contraction of the blood-vessels, with consequent fall of the temperature; dilatation of the pupil, bulging of the cornea, protrusion of the eyeball (**exophthalmos**), and widening of the palpebral fissure. At the same time, the blood-vessels to the salivary glands are contracted, and there is a secretion of *thick* saliva. The last results are due to the *vaso-constrictor and secretory* fibres. The vaso-motor and oculo-pupillary fibres, although they lie in the same trunk in the neck, do not issue from the cord by the same nerve-roots; the latter come out of the cord with the anterior roots of the 1st and 2nd dorsal nerves (dog), while section of the cord between the 2nd and 4th dorsal vertebræ produces the vaso-motor changes only. The nasal mucous membrane and lachrymal gland are influenced by the sympathetic.]

Fig. 532.

Normal ear of a rabbit. B, effect on the blood-vessels of section of the cervical sympathetic nerve.

[**Division** of the cervical sympathetic in young, *growing* animals results in hypertrophy of the ear, and increased growth of the hair on that side (*Bidder, W. Stirling*).]

[The **vago-sympathetic nerve** (dog) in the neck contains **vaso-dilator fibres** (really in the sympathetic) for the skin and mucous membranes of that side of the head. Weak stimulation of the central end of the sympathetic causes dilatation of the blood-vessels of these parts. [The local application of **nicotin** to the superior cervical sympathetic ganglion prevents stimulation below this ganglion from causing dilation of the vessels, but stimulation above the ganglion still causes the normal effect, so that Langley concludes that the vaso-dilator fibres are connected with nerve-cells in the superior cervical ganglion.] The vaso-dilator fibres of the superior maxillary nerve probably come from the same source. The centre for these nerves is in the

dorsal region of the cord between the 1st and 5th dorsal vertebræ, where the fibres pass out with the rami communicantes to enter the cervical sympathetic (*Dastre and Morat*). The vaso-dilator fibres occur in the posterior segment of the ring of Vieussens, and when they are stimulated after section of the 7th cranial nerve, there is a "pseudo-motor" effect on the muscles of the cheek and lip (§ 349).]

[**Action of Nicotin on the nerve-cells of the superior cervical ganglion.**—If nicotin be injected into a vein of a rabbit or dog, or if a 1 per cent. solution be applied locally to the superior cervical ganglion, stimulation of the cervical sympathetic *below* this ganglion, or of the ganglion itself, does not cause dilation of the pupil or constriction of the blood-vessels of the ear or face, nor does it cause secretion of saliva, but stimulation of the nerve *above* the ganglion causes these changes in a normal manner. From the results of the local application of nicotin solution to the superior cervical ganglion, it is evident that *nicotin paralyses the nerve-cells of this ganglion*, so Langley concludes that the *dilator fibres for the pupil, the vaso-constrictor fibres for the ear and head, and the secretory fibres for the glands end in cells in the superior cervical ganglion* (*Langley and Dickinson*).]

B. Thoracic and Abdominal Sympathetic.

1. The sympathetic portion of the **cardiac plexus** (§ 57, 2), which receives **accelerating** or augmentor fibres for the heart from the lower cervical and 1st thoracic ganglion (*Cl. Bernard, v. Bezold, Cyon, Schmiedeberg*). The fibres arise partly from the sympathetic and partly from the plexus around the vertebral artery (*v. Bezold, Bever*). (Compare § 370.)

2. For the vaso-motor fibres passing through the sympathetic to the extremities, skin of the trunk, and lungs (see § 371). For vaso-dilators (§ 372).

3. The cervical sympathetic and the splanchnic contain fibres which, when their central ends are stimulated, excite the **cardio-inhibitory system** in the medulla oblongata (*Bernstein*).

4. The functions of the **splanchnic** are referred to in §§ 164, 175, 276, and 371.

5. The functions of the **solar** and **mesenteric plexuses** are referred to in §§ 183 and 192. After extirpation of the cœliac ganglion, Lamansky observed temporary disturbance of digestion, undigested food being passed per anum.

[**Action of Nicotin on the solar plexus.**—The inhibitory fibres of the splanchnic end in cells of the solar plexus, and this is true for the vaso-constrictor as well as for the vaso-dilator fibres, while the splanchnic vaso-motor fibres for the kidney end in the cells of the renal plexus. The fibres of the vagus, which are motor for the intestines, do not end in the nerve-cells of the solar plexus (*Langley and Dickinson*). These results have been obtained by a study of the action of nicotin applied locally to the solar plexus, and observing the results that follow stimulation of the nerves passing to and those leading from the solar plexus; thus the local application of nicotin to the solar plexus prevented stimulation of the splanchnic nerve from causing inhibition of the movements of the stomach and intestines, while stimulation of the branches proceeding from the solar plexus caused these effects. Even when the solar plexus and the hypogastric plexus are eliminated by the action of nicotin, stimulation of the vagus still causes movements of the intestine and stomach; therefore Langley and Dickinson conclude that the vagus does not form connections with the nerve-cells at these plexuses.]

6. For the **secretory** fibres for **sweating**, see § 289, II.

7. Lastly, the abdominal portion of the sympathetic contains **motor** and **vaso-motor fibres** for the **spleen**, the **large intestine** (accompanying its arteries), **bladder** (§ 280), **ureters**, **uterus** (running in the hypogastric plexus), **vas deferens**, and **vesiculæ seminales**. *Stimulation* of all of these nerve-channels causes increased movement of the organs, but it must be remembered that the diminished supply of blood thereby produced also acts as a stimulus (§ 161). *Section* of these

nerves is followed by dilatation of the blood-vessels, with subsequent derangement of the circulation, and ultimately of the nutrition. The relation of the **suprarenal bodies** to the sympathetic is referred to in § 103, IV. [It is important to note that the medulla and cortex of these glands have totally different origins. The cortex is developed from mesoblastic cells round the blood-vessels, while the medulla represents modified sympathetic ganglia.] The **renal plexus** is referred to in § 276, while the **cavernous plexus** is treated of in § 436.

Pathological.—Considering the numerous connections of the sympathetic, we would naturally suppose that it offers an extensive area for pathological changes. Affections involving the vaso-motor system are referred to in § 371.

The **cervical sympathetic** is most frequently paralysed or stimulated by traumatic conditions, wounds by bullets or knives, tumours, enlarged lymph-glands, aneurisms, inflammation of the apices of the lungs and the adjacent pleuræ, while exostoses of the vertebræ may stimulate it in part or paralyse it in part. The phenomena so produced have been partly analysed in treating of the ciliary ganglion (§ 347, I.). **Stimulation of the cervical sympathetic** in man causes dilatation of the pupil (**mydriasis spastica**), pallor of the face, and occasionally hyperidrosis or profuse sweating (§ 289, 2, and § 288); disturbance of vision for near objects, as the pupil cannot be contracted (see *Accommodation*, § 387), and hence the spherical aberration of the lens (§ 391) must also interfere with vision; protrusion of the eyeball with widening of the palpebral fissure. **Paralysis or section of the cervical sympathetic** causes increased fulness of the blood-vessels of the side of the head, with occasional anidrosis; contraction of the pupil (**myosis paralytica**), which undergoes changes in its diameter during accommodation, but not as the effect of the stimulation of light—atropin dilates it slightly. The slit between the eyelids is narrowed, the eyeball retracted and sunk in the orbit, the cornea somewhat flattened, and the consistence of the eyeball diminished. Stimulation of the sympathetic is followed by an *increased secretion of saliva* (§ 145). The above-described symptoms have been occasionally accompanied by **unilateral atrophy of the face.**

Irritation in the area of the splanchnic, as occurs occasionally in lead poisoning, is characterised by violent pain (lead colic), inhibition of the intestinal movements (hence the persistent constipation), slowing of the heart's action, brought about reflexly, just as in Goltz's "tapping" experiment (§ 369). Irritation in the area of the sensory nerves of the sympathetic may give rise to that condition which is called by Romberg neuralgia hypogastrica, a painful affection of the lower abdominal and sacral regions, hysteralgia, neuralgia testis, which are localised in the plexuses of the sympathetic. In affections of the *abdominal sympathetic*, there may be severe constipation, with diminished or increased secretion of the intestinal glands (§ 186).

357. **COMPARATIVE—HISTORICAL.**—**Comparative.**—Some of the **cranial nerves** may be absent, others, again, may be abortive, or exist as branches of other nerves. The facial nerve, which supplies the muscles of expression in man, and is, at the same time, the nerve for facial respiratory movements, diminishes more and more in the lower classes of the vertebrata, *pari passu*, with the diminution of the facial muscles. In **birds and reptiles**, it supplies the muscles of the hyoid bone, or the superficial cervical muscles of the nape of the neck. In **amphibians** (frog), the facial no longer exists as a separate nerve, the nerve which corresponds to it springing from the trigeminus. In **fishes**, the 5th and 7th nerves form a joint complex nerve. The part corresponding to the facial (also called ramus opercularis trigemini) is the chief motor nerve of the muscles of the gill-cover, and is, therefore, the respiratory nerve. In the cyclostomata (lamprey) there is an independent facial. The *vagus* is present in all vertebrata; in fishes it gives off a large nerve, the *lateral nerve* of the body (N. lateralis), which runs along each side of the body close to the lateral canal. It is also present in the tadpole. Its rudimentary representative in man is the auricular branch. In the frog the 9th, 10th, and 11th arise together from one trunk, and the 7th and 8th from another. In fishes and amphibia, the hypoglossal is the first cervical nerve. In amphioxus, the cerebral and spinal nerves are not distinct from each other. The **spinal nerves** are remarkably similar in all classes of the vertebrata. The **sympathetic** is absent in the cyclostomata, where it is represented by the vagus. Its course is along the vertebral column, where it receives the rami communicantes of the spinal nerves. In the region of the head its connections with the 5th and 10th nerves are specially developed. In frogs, and still more so in birds, the number of connections with the cranial nerves increases.

Historical.—The vagus and sympathetic were known to the Hippocratic School. According to Erasistratus, all the nerves proceed from the brain and spinal cord; Herophilus was the first to distinguish the nerves from the tendons, which Aristotle confounded with each other. Marianus (80 A.D.) recognised seven pairs of cranial nerves. Galen was in possession of a wide range of important facts in the physiology of the nervous system (§ 140); he observed that loss of voice followed ligature of the recurrent nerves; and he was acquainted with the accessorius, and the ganglia on the abdominal nerves. The cauda equina is referred to in the Talmud;

Coiter (1573) described exactly the anterior and posterior spinal nerve-roots. Van Helmont († 1644) states that the peripheral motor nerves also give rise to impressions of pain, and Cesalpinus (1571) remarks that interruption of the blood-stream makes the parts insensible. Thomas Willis described the chief ganglia (1664). In Des Cartes there is the first indication of a study of reflex movements; Stephen Hales and Robert Whytt showed that the spinal cord was necessary for such acts. Prochaska described the reflex channels, [while Marshall Hall established the doctrine of reflex, or, as he called them, "diastaltic" actions]. Duverney (1761) discovered the ciliary ganglion. Gall traced more carefully the course of the 3rd and 6th nerves, and also the spinal nerves into the grey matter. Hitherto only nine nerves of the brain have been enumerated; Sömmerring (1791) separated the facial from the auditory nerve, Andersch (1797) the 9th, 10th, and 11th nerves.

Physiology of the Nerve-Centres.

358. **GENERAL.**—[The nerve-fibres and nerve-cells constitute the elements out of which nerve-centres are formed, being held together by connective-tissue. In the process of **evolution**, groups of nerve-cells with connecting fibres are arranged to constitute nervous masses, whereby there is a corresponding integration of function. Thus, with structural integration there is a functional integration. When the structure suffers, so also does the function, and those parts which are most evolved, as well as those actions which have to be learned by practice, are the first to suffer during the **dissolution** of the nervous system.]

General Functions.—The central organs of the nervous system are in general characterised by the following properties:—

1. They contain **nerve-cells**, which are either arranged in groups in the interior of the central organs of the nervous system, or embedded in the peripheral branches of the nerves. [Nerve-cells are centres of activity, originate impulses and conduct impulses as well, while nerve-fibres are chiefly conductors.]

2. The nerve-centres are capable of discharging **reflexes**, *e.g.*, reflex-motor, reflex-secretory, and reflex-inhibitory acts (fig. 511).

3. The centres may be the seat of **automatic excitement**, *i.e.*, they may manifest phenomena, without the application of any *apparent* external stimulus. The energy so liberated may be transferred to act upon other organs. This automatic state of excitement or stimulation may be *continuous*, *i.e.*, may be continued without interruption, when it is called tonic automatic or **tonus**; or it may be *intermittent*, and occur with a certain rhythm (*rhythmical automatic*).

4. The central organs are **trophic centres** for the nerves proceeding from them; they may also perform similar functions for the tissues innervated by them.

5. The **psychical activities** are dependent upon an intact condition of the ganglionic central organs. These various functions are distributed over different centres.

[The term "**centre**" is merely applied to an aggregation of nerve-cells so related to each other as to subserve a certain function, but, inasmuch as these cells are in relation to each other and with other cells in many ways, various combinations of them may result; again, we have also to take into account the greater or less resistance in some paths than in others, so that the variety of combinations which these cells may subserve is enormous. These cells give off processes which branch, and come into relation with processes from other cells. Thus, innumerable ways are opened up to nervous impulses by these combinations, so that in a certain way we may regard a cell as a junction of these conducting fibres, or a "shunt" whereby an impulse may be shunted on to one or other branch in the direction of least resistance, or in the best beaten path, as it were, while there may be a "block" in other directions.]

[In connection with the histology of the central nervous system we have to study:—

A. The nervous constituents.
- (1) Nerve-fibres.
- (2) Nerve-cells.

B. Non-nervous constituents.
- (1) Vessels (blood and lymph).
- (2) Epithelium.
- (3) Sustentacular tissue.
  - (*a*) Connective-tissue.
  - (*b*) Neuroglia.]

The Spinal Cord.

359. **STRUCTURE OF THE SPINAL CORD.**—[The key to the study of the central nervous system is to remember that it begins as an involution of the epiblast, and is originally tubular, with a central canal, dilated in the brain-end into ventricles. In the spinal cord there are three concentrated parts: first, the columnar ciliated epithelium, outside this the central grey tube, and, covering in all, the outer white conducting fibres (*Hill*).]

[**Structure.**—The spinal cord forms a more or less cylindrical column 40–50 cm. (18 inches) in length, reaching from the lower end of the medulla oblongata or bulb at the level of the first cervical vertebra to the first or second lumbar vertebra, where it ends in a slender filament, the filum terminale, which lies amongst a leash of nerve-roots called the cauda equina. Above, the cord is continuous with the medulla oblongata or bulb at the margin of the foramen magnum. The whole cord is enclosed in the vertebral canal, and is further protected by its "**membranes.**" Although the cord does not present uniformity of characters throughout its extent, still there are certain general features common to it as a whole.

[It is invested by **membranes**—the **pia mater**, composed of two layers and consisting of connective-tissue with blood-vessels, being firmly adherent to the surface of the cord and sending septa into the substance of the latter. Both layers dip into the anterior median fissure, and only the inner one into the posterior median groove. The **arachnoid** is a more delicate membrane and non-vascular, while the **dura mater** is a tough membrane lining the vertebral canal, and forming a theca or protective coat for the cord (§ 381).]

The spinal cord consists of white matter externally, giving the cord its opaque, white appearance, and grey matter internally; and in each the **grey mater** has the form of two crescents)–(placed back to back [or a capital H]. In each crescent we can distinguish an **anterior** (*co.a*), a **posterior horn** (*co.p*), and a middle part, cervix or neck. An isthmus or **grey commissure** connects the two crescents across the middle line. In the centre of this grey commissure is a canal—**central canal**—which runs from the calamus scriptorius downwards; it is lined throughout by a single layer of ciliated cylindrical epithelium in the fœtus, the cilia not being visible in the adult, and the canal itself is the representative of the embryonal "medullary tube" (figs. 533, 540). [The central canal is the remains of the neural canal of the embryo, which was originally the comparatively wide neural canal of the embryo. Some observers doubt whether the cilia are really true cilia. This epithelium is epiblastic in origin.] [The part of the grey commissure in front of this canal is called the **anterior grey commissure**, and the part behind, the **posterior grey commissure**. In front of the grey commissure, and between it and the base of the anterior median fissure,

are bundles of white nerve-fibres passing in a horizontal or oblique direction from the anterior column of one side to the grey matter of the anterior cornu of the opposite side (fig. 533). These decussating fibres constitute the **anterior white commissure.**]

The **white matter** surrounds the grey, and is arranged in several **columns** [**anterior, lateral,** and **posterior**—by the passage of the nerve-roots to the cornua (figs. 533, 540)]. Along the anterior surface of the cord there runs a well-marked fissure, which dips into the cord itself, but does not reach the grey matter, as a mass of white matter—the **white commissure**—runs from one side of the cord to the other. Between this fissure, known as the **ventral** or **anterior median fissure,** and the line of exit of the anterior roots of the spinal nerves, lies the **anterior column** (*f.a*); the white matter lying laterally between the origin of the

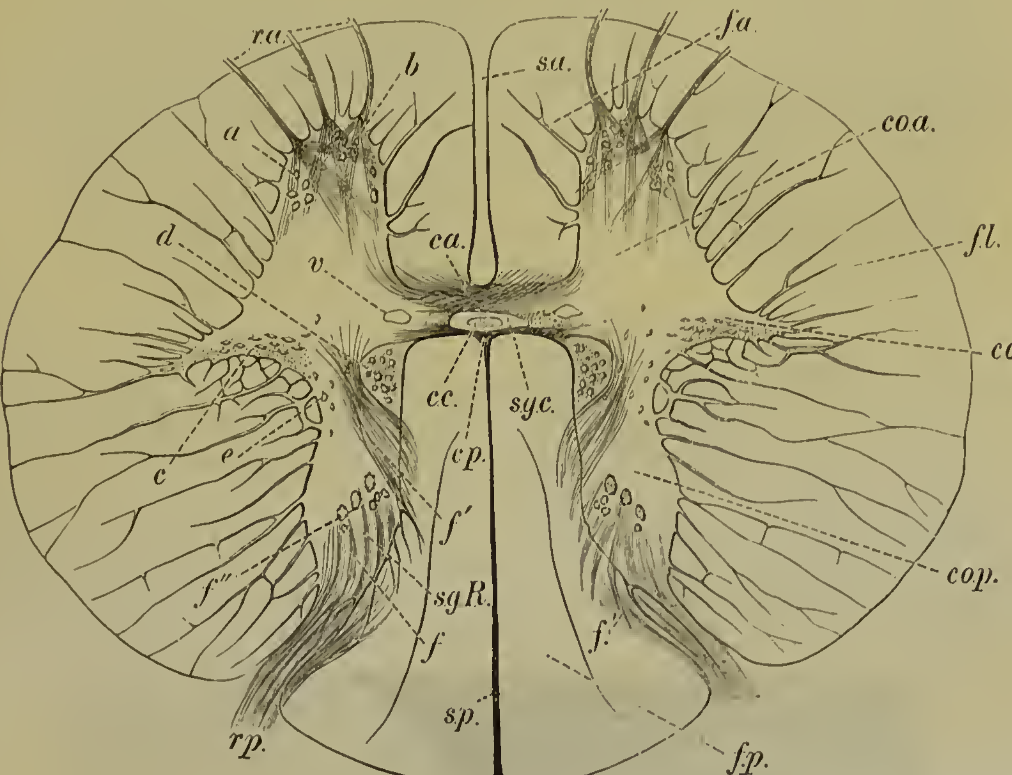


Fig. 533.

Transverse section of the human spinal cord at the level of the 8th dorsal vertebra ; × 10. *s.a*, anterior longitudinal fissure ; *s.p*, septum posterium ; *c.a*, anterior commissure ; *s.g.c*, substantia gelatinosa centralis ; *c.c*, central canal ; *c.p*, posterior commissure ; *v*, vein ; *co.a*, anterior horn ; *co.l*, lateral horn, and behind it the processus reticularis ; *co.p*, posterior horn ; *a*, antero-lateral, *b*, antero-median group of ganglionic cells ; *c*, cells of the lateral horn ; *d*, cells of Clarke's column ; *e*, solitary cells of the posterior horn ; *r.a*, anterior root ; *r.p*, posterior root, with *f* its bundle of fibres ; *f'*, postero-internal bundle ; *f''*, longitudinal fibres of the posterior cornu ; *s.g.R*, gelatinous substance of Rolando ; *f.a*, anterior column ; *f.l*, lateral column ; *f.p*, posterior column.

anterior and posterior roots of the spinal nerves is the **lateral column** (*f.l*), while the white matter lying between the line of origin of the posterior roots of the so-called **dorsal** or **posterior median fissure** is the **posterior column** (*f.p*). [The posterior median fissure is not a real fissure, but is filled up with the inner layer of the pia mater, which dips down from the under surface of this membrane quite to

the grey matter of the posterior commissure.] Each posterior column, in certain regions of the cord, may be subdivided into an inner part lying next the fissure, the **postero-median** or **Goll's column**, or the **inner root-zone** (*Charcot*, fig. 533, *f*); and an outer larger part next the posterior root, known as the **postero-external** or **Burdach's column**, or the **outer root-zone** (*Charcot*, fig. 533, *f'*).

The **white matter** consists chiefly of medullated fibres without the sheath of Schwann, but provided with the neuro-keratin sheaths of Kühne and Ewald (§ 321), the fibres themselves being chiefly arranged *longitudinally*. [The incisures of Schmidt exist in these fibres, and can be demonstrated by the interstitial injection of osmic acid (*Ranvier*). The fibres are also provided with Ranvier's nodes.] The

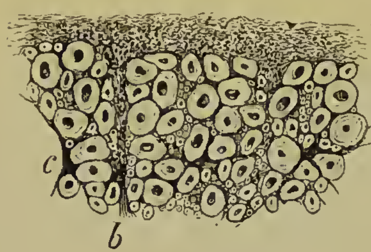


Fig. 534.

Fig. 535.

Fig. 534.—Transverse section of the white matter of the cord; ×150. *a*, peripheral layer. Besides the transverse sections of the nerve-fibres, large and fine, there are three branched connective-tissue corpuscles (*c*). Fig. 535.—Multipolar nerve-cells from the grey matter of the anterior horn of the spinal cord (ox). *a*, nerve-cell; *b*, axis-cylinder; *c*, grey matter; *d*, white matter of column; *c*, *c*, branches of cells.

nerve-fibres of the nerve-roots, as well as those that pass from the grey matter into the columns, have a transverse or oblique course. There are also decussating fibres in the anterior or white commissure. [In a transverse section of the white matter of the spinal cord, the nerve-fibres are of different sizes, and appear like small

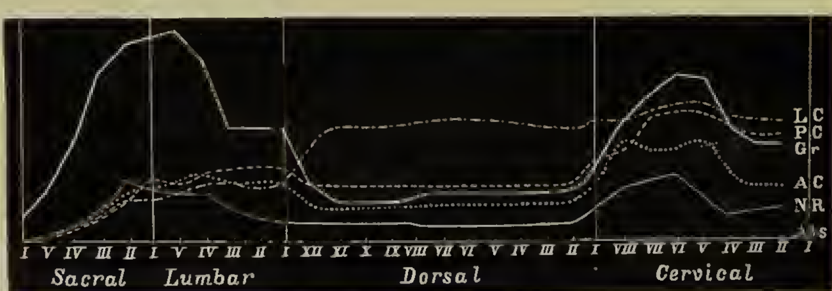


Fig. 536.

Diagram of the absolute and relative extent of the grey matter, and of the white columns in successive sectional areas of the spinal cord as well as the sectional areas of the several entering nerve-roots. NR, nerve-roots; AC, LC, PC, anterior, lateral, and posterior columns; Gr, grey matter.

circles with a rounded dot in their centre—the axis-cylinder; the latter may be stained with carmine or other dye (fig. 534). They are smallest in the postero-median or Goll's column, and largest in the crossed and direct pyramidal tracts, which are motor. The white substance of Schwann, especially in preparations

hardened in salts of chromium, often presents the appearance of concentric lines. Fine septa of connective-tissue carrying blood-vessels lie between groups of the nerve-fibres, while here and there between the nerve-fibres may be seen branched neuroglia corpuscles. Immediately underneath the pia mater there is a pretty thick layer of neuroglia, which invests the prolongations of the pia into the cord (fig. 534, *a*).]

[The **grey matter** differs in shape in the different regions of the cord, and so does the grey commissure (fig. 537). The latter is thicker and shorter in the cervical than in the dorsal region, while it is narrow in the lumbar region. The amount of grey matter undergoes a great increase opposite the origins of the large nerves, the increase being most marked opposite the cervical and lumbar enlargements. Ludwig and Woroschiloff constructed a series of curves from measurements by Stilling of the sectional areas of the grey and white matter of the cord, as well as of the several nerve-roots. These curves have been arranged in the annexed convenient form by Schäfer after Woroschiloff (fig. 536)]:—

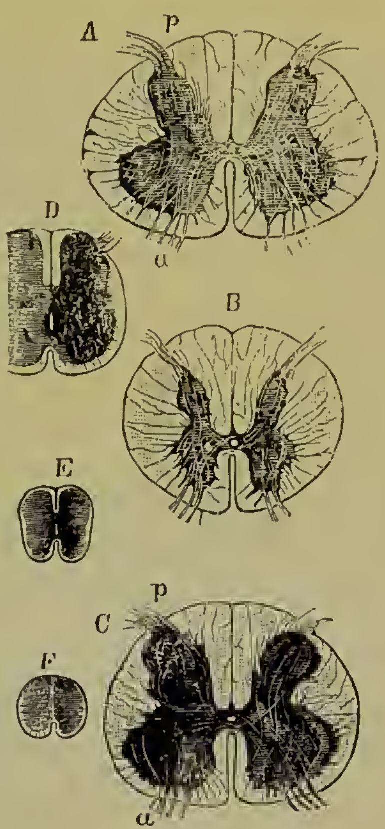


Fig. 537.

Transverse sections of the spinal cord in different regions. A, through the middle of the cervical; B, the dorsal; C, the lumbar enlargement; D, upper part of the conus medullaris; E, at the 5th sacral vertebra; F, at coccyx; A, B, C, enlarged twice; D, E, F, thrice; *a*, anterior, *p*, posterior root.

[In the **cervical region**, the lateral white columns are large, the anterior cornu of the grey matter is wide and large, while the posterior cornu is narrow; Goll's column is marked off by a depression and a prolongation of the pia mater; the cord itself is broadest from side to side. In the **dorsal** region, the grey matter is small in animals, and both cornua are narrow and of nearly equal breadth, while the cord itself is smaller and cylindrical. In it the intermedio-lateral and posterior vesicular groups of cells are distinct. They have probably relations to viscera. The commissure, and therefore the central canal, lie well forward between the crescents. In the **lumbar** region the grey matter is relatively and absolutely greatest, while the white lateral columns are small, the central canal in the commissure being nearly in the middle of the cord. In the **conus medullaris**, the grey matter makes up the great mass of it, with a few white fibres externally (figs. 537, 538).]

The **anterior cornu** of the grey matter is shorter and broader, and does not reach so near to the surface as the posterior; moreover, each anterior nerve-root arises from it by several bundles—it contains several groups of large multipolar ganglionic cells (fig. 535); the **posterior cornu** is more pointed, longer, and narrower, and reaches nearer to the surface, the posterior root arising by a single bundle at the postero-lateral fissure; while the cornu itself contains a few small fusiform nerve-cells, and is covered by the **substantia gelatinosa** of Rolando, which is in part an accumulation of neuroglia.

[The **substantia gelatinosa** on the posterior cornu is marked by striation where the posterior root-fibres traverse it. It contains some connective-tissue cells and some fusiform nerve-cells, especially near the margins. The substance itself stains deeply with carmine.]

[The outer margin of the grey matter near its middle is not so sharply defined from the white matter as elsewhere; and, in fact, a kind of anastomosis of the grey matter projects into the lateral column, especially in the cervical region, constituting the **processus reticularis** (fig. 540).]

[**Arrangement of Nerve-Cells.**—The nerve-cells are arranged in several groups, forming columns more or less continuous. There are those of the anterior and posterior horns, those of the lateral column (intermedio-lateral), and the posterior vesicular column of Clarke (fig. 538). The anterior and posterior groups exist as continuous columns along the entire cord. The cells in the **anterior cornu** are subdivided into smaller groups, which vary in the different regions of the cord. There is an *inner or median group* near the anterior angle of the cornu. It is the smallest group, and is absent in the lumbar region. Near the anterior edge is the *anterior group*, and in the external part of the cornu is the *antero-lateral group*. These two groups are often united, as in the mid-cervical region. There is usually a third large group—the *external* or *postero-lateral* in the posterior outer angle of the anterior cornu. The cells of the anterior horn being very large (67 to 135 μ).

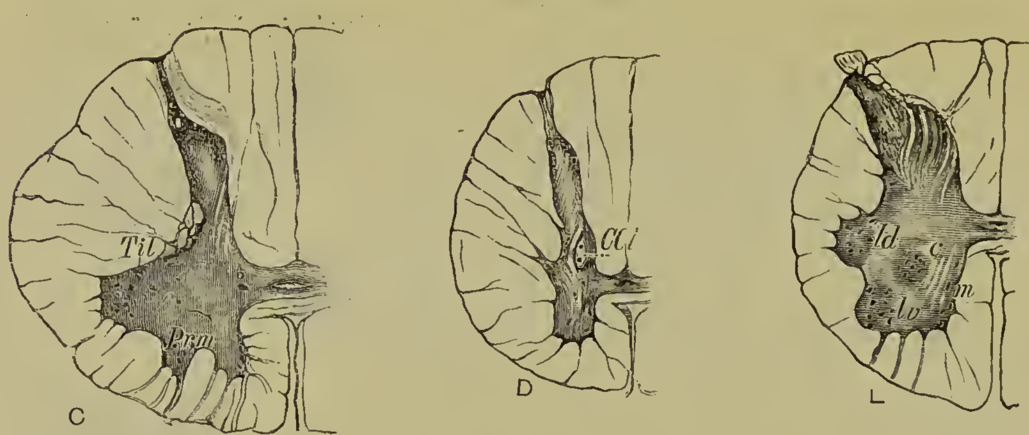


Fig. 538.

C, Transverse section of the human spinal cord at the level of the 6th cervical nerves; *Prm*, median process of the anterior horn; *Til*, intermedio-lateral tract or lateral horn; D, at the level of the 3rd dorsal nerves; *CCl*, Clarke's column; L, at the level of the 5th lumbar nerve; *m*, median; *lv*, latero-ventral; *ld*, latero-dorsal; *c*, central groups of cells of anterior horn.

The cells of the **posterior cornu** usually do not lie in groups, but singly, hence they have been called **solitary cells.** They are bipolar or fusiform cells, and are about 18 μ in diameter. They lie especially at the outer side of the base of the cornu of the grey matter, and are placed with their long axis horizontal, and their processes are directed forwards and backwards. Those of the lateral column are distinct, except in the lumbar and cervical enlargements, where they blend with the anterior horn. The **vesicular column of Clarke** (cells 40 to 90 μ) is discontinuous, and is limited to (1) the thoracic region, (2) cervico-cranial region, (3) sacral region, being most conspicuous in (1), where it corresponds absolutely to the outflow of visceral nerves (*Gaskell*). In the sacral region it is said by some observers to correspond to the "sacral nucleus of Stilling," while in the cervical region it begins in the dog at the 2nd cervical nerve, forming the cervical nucleus, being continued above into the nuclei of the vagus and glosso-pharyngeal nerves. It is important to note that the vesicular column of Clarke (fig. 538, *CCl*) does not extend throughout the cord. A small group of cells exists opposite the 2nd and 3rd cervical nerve; it extends as a continuous column from the 8th cervical to the 3rd lumbar nerve, so that it is best developed in the thoracic region.

[**Connections of Clarke's Column.**—Gaskell showed that a large number of *fine medullated nerve* fibres leave the cord in the anterior roots of the dorsal nerves (§ 356), and as the distribution of Clarke's column corresponds to this outflow of fine fibres, it was suggested that these fine medullated fibres—or, as Gaskell called them, **leucenteric fibres**, were connected with the cells of Clarke's column. There is reason to believe, however, that this is not the case. The cells of Clarke's column are large cells (90 μ; the smallest is 40 μ in diameter). Some of the fibres which come from the lumbar and sacral nerves, and form part of the postero-external column, pass towards the cells of Clarke's column, where they break up into a brush or pencil of fibrils, to form a fibrillar plexus or spongy network of fine nerve fibrillæ around the cells of Clarke's column (*Mott*). Cayal has also shown the existence of an enormous number of fibrils,—according to him, not forming a plexus around these cells. The cells are bipolar, and it is suggested by Mott that their distal connections are with fibres of the postero-external column as also that to them are transmitted various afferent impulses coming from viscera, and it may be from tendons and other parts, and that these impulses pass *viâ* the direct cerebellar tract to the cerebellum. In locomotor ataxia the fibrillar thicket of fibrils around these cells is degenerated. The average size of the cells at birth is about 25 μ–30 μ, at two years 60 μ, and in the adult 70 μ. From the cells of Clarke's column, there proceed large fibres, which run upwards, slightly forwards, and then outwards through the lateral column to reach the direct cerebellar tract of the same side, whence they proceed to the cerebellum. The direct cerebellar fibres of the cord do not degenerate unless Clarke's column be injured. These cells appear to act as stations for afferent impulses between the peripheral nervous system and the cerebellum (*Ross*, *Mott*).]

[The **intermedio-lateral tract** of cells is also best developed in the thoracic region (fig. 538, *Til*). In the cervical region it fuses with the lateral group of cells in the anterior cornu. It cannot be traced in the lumbar region.]

[The cells of the intermedio-lateral tract confined to the dorsal region are arranged in groups of eight to twelve bipolar cells, with their long axis vertical or more or less oblique. The smaller cells are about 20 μ in diameter, and seem to be identical with the solitary cells of the posterior cornu, the larger ones are 30 μ in diameter, and these cells attain their full size, or nearly so, at birth. Mott considers that these cells correspond in form and size with the cells of the vagus nucleus, and that these cells give origin to the fine medullated or leucenteric fibres that leave the cord by the anterior roots of the dorsal nerves (p. 796), *i.e.*, to the splanchnic efferent fibres of the anterior roots of the dorsal nerves.]

The **multipolar ganglion cells** are largest, and arranged in groups in the anterior horns of the grey matter (fig. 540—"**motor ganglionic cells**"). [They also occur in the lateral process and in the processus reticularis. It is to be noted that the cells become more branched as we proceed upwards amongst the vertebrata. These cells usually contain pigment-granules, and, according to Pierret, their size has a direct relation to the length of the nerve-fibre proceeding from them; so that they are largest in the lumbar enlargement, smaller in the cervical enlargement, and smallest in the dorsal region. Smaller spindle-shaped ("**sensory**") cells occur in much smaller numbers in the grey matter of the posterior horn. The cells of **Clarke's column** (fig. 539) are smaller (30–60 μ) and are usually arranged with their long axis in the long axis of the cord. The processes are fewer, but one is generally directed towards the head, and some towards the caudal end of the body. They usually contain pigment, which is generally disposed towards the cerebral pole of the cell.]

[In a **longitudinal section** of the cord (fig. 541), these cells are seen to be arranged in columns, the large multipolar cells in the anterior horn (*m*); in the same section are shown the longitudinal direction of the nerve-fibres in the anterior

(*a*) and posterior white columns (*c*), the horizontal direction of the fibres of the anterior and posterior nerve-roots (*b* and *f*).

[**Outlying Cells of the Cord.**—Beisso, Schiefferdecker, and more recently Sherrington, have shown that in certain situations in the anterior lateral and posterior columns of the mammalian cord, ganglionic cells lie outside the grey matter in the surrounding white substance. In the Alligator there is a remarkable group of ganglionic cells lying quite at the periphery of the antero-lateral column, and quite removed from the grey matter (*Berger*, *Gaskell*); its significance is quite unknown.]

The **grey matter** contains an exceedingly delicate fibrous thicket of the finest nerve-fibrils, which is produced by the repeated division of the protoplasmic pro-

Fig. 539.

Fig. 540.

Fig. 539.—Nerve-cell from Clarke's column (horse). The arrow indicates the cerebral end.
Fig. 540.—Transverse section of the spinal cord (lower dorsal). A, L, P, anterior, lateral, and posterior columns; A.M.F., P.M.F., anterior and posterior median fissures; *a*, *b*, *c*, cells of the anterior horn; *d*, posterior cornu and substantia gelátinosa; *e*, central canal; *f*, veins; *g*, anterior root bundles; *h*, posterior root bundles; *i*, white commissure; *j*, grey commissure; *l*, reticular formation.

cesses of the multipolar ganglionic cells. Many medullated nerve-fibres—chiefly of the fine variety—traverse and divide in the grey matter and become non-medullated. Many of them split up into terminal fibrils, branches of the axis cylinder. Some of them merely pass through the grey matter of the non-medullated fibres and terminate in the nervous network or thicket of the grey matter. Fibres pass from the grey matter of one side to that of the other through the commissures in front of and behind the central canal.

[By means of Weigert's method of staining medullated nerve-fibres (p. 653), it has been proved that numerous fine medullated nerve-fibres exist in the grey substance.]

[The **anterior root** enters in several bundles of coarse fibres which diverge

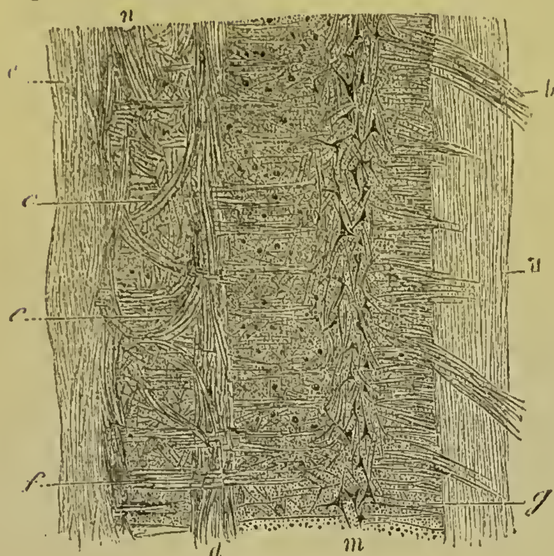


Fig. 541

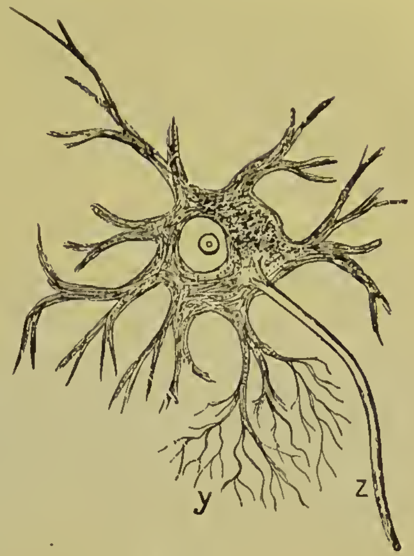


Fig. 542.

Fig. 541.—Longitudinal section of the human spinal cord. *a*, anterior, *c*, posterior, *d*, lateral white columns; *b*, anterior, *c*, posterior nerve-roots; *f*, horizontal (pyramidal) fibres passing to *m*, cells of anterior cornu; *n*, oblique fibres of posterior root. Fig. 542.—Multipolar nerve-cell, from the anterior horn of the spinal cord. *z*, axis-cylinder process; *y*, branched processes.

before they reach the grey matter. Most of the fibres end in the large motor nerve-cells in the anterior cornu or its lateral process (fig. 543, *a*, *b*, *c*, *d*, *e*). But the fibres diverge in all directions, some of the fibres of the bundle nearest the middle line (3) end in the laterally placed cells (*c*); a part (4) crosses the anterior commissure to end in cells on the opposite side (*d*). Some of them (6) run upwards to become connected with motor cells lying further up the cord. Some of the fibres present in the anterior roots, *e.g.*, the vaso-motor and secretory fibres, appear not to be connected with the nerve-cells of the anterior cornu. Perhaps all the motor fibres for the skeletal muscles are so connected, so that each motor nerve-fibre is merely the prolongation of the unbranched axis-cylinder process of a nerve-cell.]

[The **posterior root** enters as a single bundle (fig. 533), composed of finer fibres intermixed with bundles of thicker ones.]

[Two distinct bundles enter the cord. There is an outer **lateral bundle**, or **outer radicular fibres**, which curve into the longitudinal fibres, so that they are cut across in a transverse section, but they again take a horizontal course and enter

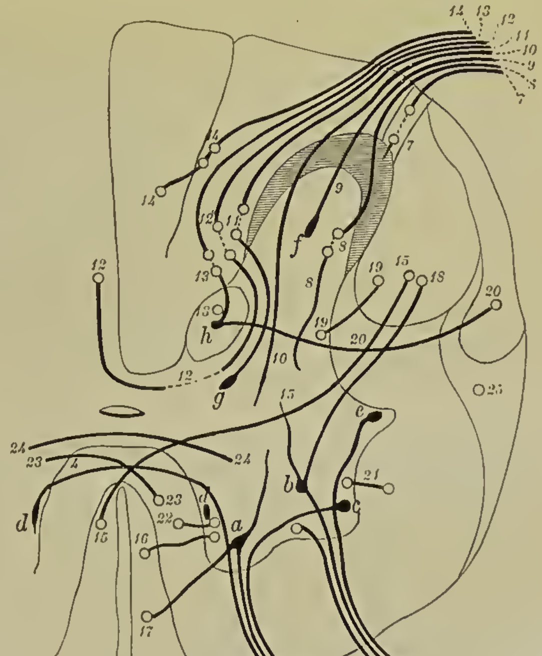


Fig. 543.

Scheme of the course of the fibres in the spinal cord. The longitudinal fibres are indicated by small circles, while the nerve-cells are black.

the substantia gelatinosa. The finest fibres in the bundle are usually placed most laterally. Lying on the inner side of this is the larger bundle, constituting the **inner radicular fibres** of the **median bundle.** The lateral bundle divides into an **intermediate** or **central bundle,** and a small external lateral bundle (7). The small external lateral bundle consists of fine fibres, which ascend for a short distance in the cord, and form the posterior marginal zone or Lissauer's zone (fig. 557). They enter the grey matter higher up and terminate in the cells of the grey matter of the posterior horn. The **central** fibres, which are coarse fibres (8 to 10), pass into the substantia gelatinosa, where they divide into several strands, some of which pass into the central part of the grey matter (10), while others (8) pass upwards and downwards in a longitudinal direction, and form the "longitudinal bundles of the posterior horn." Some of the fibres (9) perhaps end in the nerve-cells (f) in the posterior cornu. The inner **median bundle** or **internal radicular fasciculus** (11 to 14), composed of comparatively coarse fibres, sweeps through the postero-external column—hence this column is also called the posterior root-zone—and, after running a longitudinal course in the white matter, enters the grey substance of the posterior cornu. Some fibres (11) pass to the small fusiform cells (g); and others (13) pass to be connected with the cells of Clarke's column (h), when it is present. From the cells of Clarke's column, fibres seem to pass to the direct cerebellar tract (20). Some of the fibres (12) pass into the posterior grey commissure, to reach the opposite side. This so far only accounts for a part of the fibres. Some of them (8 to 10) are concerned in the formation of the fine nerve thicket in the grey matter, whereby, perhaps, they become connected with the cells in the anterior cornu. It is asserted that some of the fibres (14) ultimately pass into Goll's column. Many of the fibres in the posterior root have been proved to be directly connected with nerve-cells, *e.g.*, in Petromyzon by Freund, and in the Proteus by Klaussner.]

Fig. 544.

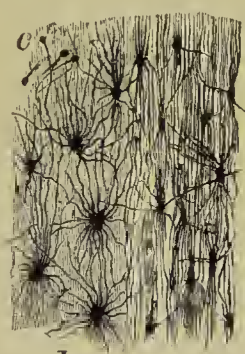


Fig. 545.

Fig. 544.—Isolated connective-tissue corpuscle or "glia-cell" from the human spinal cord ; × 800. Fig. 545.—Longitudinal section of the spinal cord. a, white, b, grey matter ; c, crystals of mercuric chloride. Prepared by Golgi's mercuric chloride method ; × 80.

[**Size of Nerve-Cells and Nerve-Fibres.**—There is reason to believe that the size of nerve-fibres bears a relation to the size of the nerve-cell from which it arises. It has been suggested by Schwalbe that nerve-fibres which run a long course are larger than those running a short course. This is not invariably the case (p. 653).]

Neuroglia.—The **connective-tissue** of the spinal cord arises in part from the pia mater and passes into the white matter, carrying with it blood-vessels, and forming septa, which separate the nerve-fibres into bundles. [The connective-tissue of the central nervous system is so far peculiar, that the intercellular substance is reduced to a minimum. It consists of a reticulated connective-tissue composed of fine fibres, which form a network. Fig. 544 shows one of the cells, "**glia-cells**"

or "**Deiter's cells**," isolated. It consists of a small, granular, nucleated body, with numerous excessively fine, slightly branched, stiff processes. The processes form a sustentacular tissue for the nerve-fibres and blood-vessels. The arrangement and distribution of these cells is best seen in sections of a cord hardened by Golgi's method in corrosive sublimate solution (fig. 545). In some situations, *e.g.*, the white matter of the cerebrum and cerebellum, the cells are smaller and more angular, and the processes are often connected with the outer coat of the blood-vessels. On the whole, the connective-tissue is much finer in the brain than in the cord. Chemically, these glia-cells consist of neuro-keratin, and they seem to be of epiblastic origin, thus differing from ordinary connective-tissue, which is mesoblastic in origin.] The central canal is surrounded with a denser layer of this tissue, known as the "**central ependyma**," which stains deeply with carmine, and is very like the substantia gelatinosa in its structure (p. 767). We must distinguish from this form of connective-tissue that special form in the grey matter to which Virchow gave the name of **neuroglia**. It is specially adapted to fill up the spaces left by the other elements, and without interfering with the exchange of fluids serves to hold the elements together. It is an excessively finely granular ground-substance in the grey matter. It is also an intercellular substance, but in the adult the cells to which it owes its origin are no longer to be found. It is doubtful, from its chemical nature, if it is really to be reckoned along with the connective-tissues. It seems to be rather a tissue *sui generis*, belonging to the nervous system, and it is present in very small amount. It seems to consist of neuro-keratin, and the cells are epiblastic in origin, being derived from the cells of the epiblast.] The neuroglia is also abundant on the sides and apex of the posterior horns, where it is called the **gelatinous substance of Rolando**.

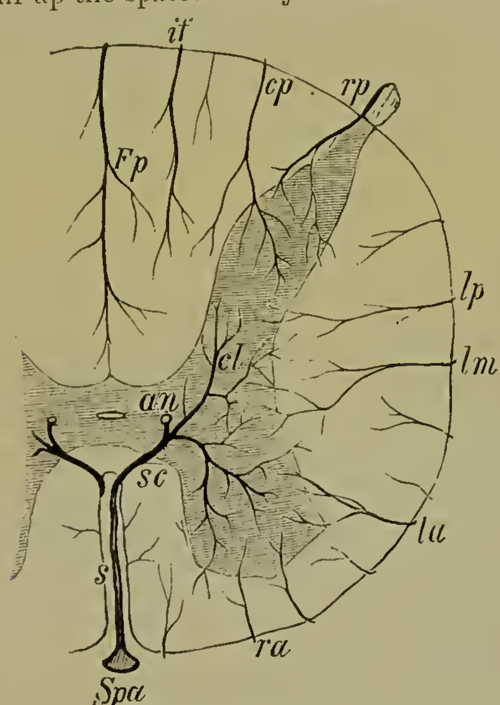


Fig. 546.

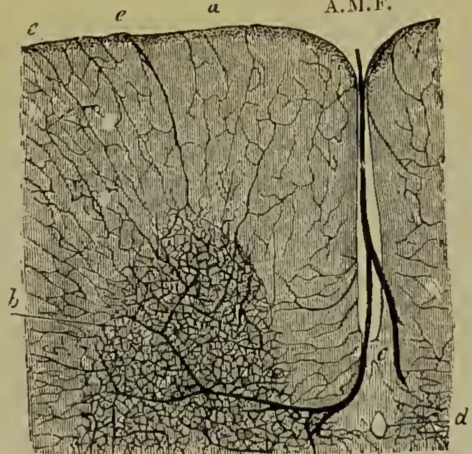


Fig. 547.

Fig. 546.—Semi-diagrammatic arrangement of the arteries in the spinal cord. *Spa*, anterior spinal; *s*, sulcine artery; *sc*, sulco-commissural; *an*, its anastomosing branch; *cl*, to Clarke's column; *Fp*, posterior fissure; *ra*, *rp*, branches along anterior and posterior roots; *cp*, for post. cornu; *if*, interfunicular; *la*, *lm*, *lp*, anterior, median, and posterior lateral.
Fig. 547.—Injected blood-vessels of the spinal cord.

[**Blood-Vessels.**—The spinal cord is partly supplied with blood by arteries from the vertebrals, and partly by branches of the intercostal, lumbar, and sacral arteries, which reach it through the intervertebral foramina, and pass to the cord along the anterior and posterior roots.]

[**Blood-Vessels.**—The anterior median artery (or anterior spinal) (fig. 546) gives off branches, which dip into the fissure of the same name, pass to its base, and, after perforating the anterior commissure, divide into two branches, one for each mass of grey matter, and each branch in turn splits into three, which supply part of the anterior median, and posterior grey matter. The arteries lying in the sulci are called **arteriæ sulci** (*s*) by Adamkiewicz. In the grey matter there is usually a special branch to Clarke's column (*cl*). The **vaso-coronary** arteries include all those arterial branches which proceed from the periphery into the white matter; the finer branches pass only into the white matter, but the larger into the grey substance. The largest branch is the artery of the posterior fissure (*Fp*), which passes along the posterior septum and reaches almost to the commissure, giving branches in its course. There is a large artery between the column of Goll and the postero-external column, viz., the interfunicular artery (*if*). Arteries enter along the anterior and posterior roots (*ra, rp*). There are also a median lateral artery (*lm*), and an anterior and posterior lateral (*lp, la*), which enter the lateral column. The general result is that the grey matter is much more vascular than the white, as is shown in fig. 547. Some small vessels come from the pia and send branches to the white matter, and unbranched arteries to the grey matter, where they form a capillary plexus. The blood-vessels are surrounded by **perivascular lymph-spaces** (*His*). With regard to the blood-vessels supplying the cord as a whole, Moxon has pointed out that, owing to the cord not being as long as the vertebral canal, the lower nerves have to run down within the vertebral canal, before they emerge from the appropriate intervertebral foramina. As **re-enforcing arteries** enter the cord along the course of these nerves, necessarily the branches entering along the course of the lumbar and lower dorsal nerves are long, and this, together with their small size, offers considerable resistance to the blood-stream. Hence, perhaps, the reason why the lower part of the cord is so apt to be affected by various pathological conditions.]

[**Recent researches of Golgi, Ramón y Cayal, and Kölliker.**—Golgi's method was adopted by all these observers, viz., prolonged steeping of the nerve-centres in

Fig. 548.

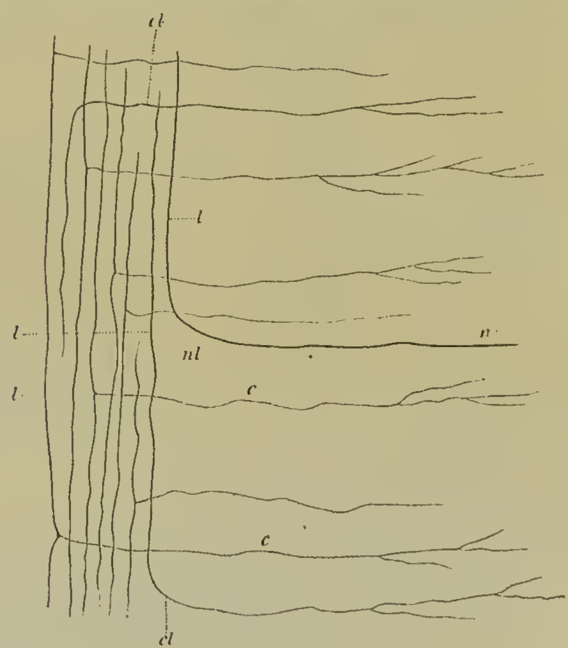


Fig. 549.

Fig. 548.—Longitudinal section of the cord in the cervical region of a sheep's embryo, 22 cm. long, to show the division of the posterior nerve-fibres after entering the cord. Fig. 549.—Lateral column of a new-born rabbit; *c*, collateral fibres; *cl*, bending round of the longitudinal fibres to end in the grey matter; *n*, axis-cylinder process of a nerve-cell bending in amongst the longitudinal fibres of the white column.

a dilute solution of silver nitrate, after previous hardening in Müller's fluid, or other fluid containing a chromium salt, or by the rapid hardening method—viz., a mixture of potassium bichromate and osmic acid. The nerve-cells and the axis-cylinders become black; but all the cells or axis-cylinders in any piece of tissue are by no means affected by the reagent. Ramón y Cayal made the great advance

of using the embryonic nerve-centres, and results have been obtained on them that are not so easily obtained in the adult. The axis-cylinders stain best before the myelin is developed, and hence the reason why embryonic nerve-centres stain so well before the myelin covers the axis-cylinders.]

[The above description of the cord is based on a study of the cord prepared by the ordinary methods, but Golgi's method reveals further complications in the structure of the cord, some of which are here noted. The **sensory nerve-fibres** on entering the white matter divide into an ascending and a descending fibre, which run longitudinally in the posterior column and in the posterior marginal zone, just superficial to the substantia gelatinosa (fig. 548, S). The longitudinal fibres have been traced for a distance of 4–6 cm., but a large number of them bend round and enter the grey matter, and end free in fine branches, without forming any connections with nerve-cells (fig. 550). All the sensory or afferent longitudinal fibres in the posterior column give off at nearly a right angle fibres called by Ramón y Cayal, who discovered them, **collateral fibres**, which penetrate into the grey matter, and run to all its parts, and split up into numerous fibrils and end free (figs. 549 *c*, *l*, 552). The free fibrillar terminations of these collateral fibres are specially numerous in the ventral portion of the substantia gelatinosa and Clarke's column, and in the ventral and lateral parts of the anterior horns, to which pass numerous bundles of collateral fibres.]

The nerve-fibres of the **anterior root** spring from large and small multipolar nerve-cells from all parts

Fig. 550.

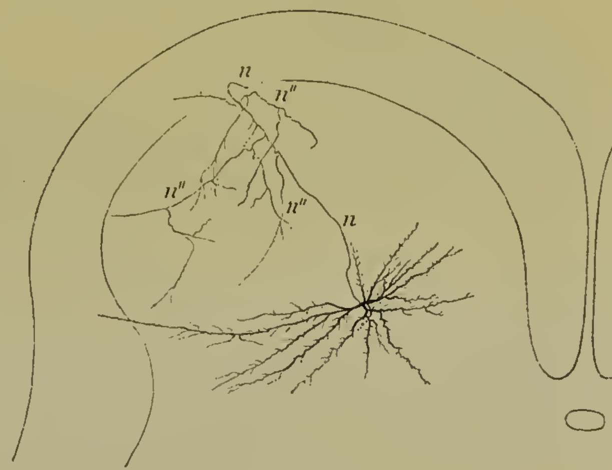


Fig. 551.

Transverse section of the cervical enlargement of the cord of a new-born rabbit with the collateral fibres from all the columns of the cord, and the anterior and posterior commissures, *ca* and *cp*. Fig. 551.—A nerve-cell in the anterior cornu of the lumbar region of an ox-embryo, 20 cm. long; *n*, axis-cylinder process, passing at *n′* into a longitudinal fibre of the anterior column; *n″*, much branched lateral processes of *n*. All prepared by the silver nitrate method of Golgi.

of the anterior cornu (fig. 552), but it appears that the axis-cylinder process of the nerve-cell gives off a few lateral branches (fig. 551).

The **anterior and lateral columns** consist in part of fibres which spring from nerve-cells in all regions of the grey matter (fig. 550). These cells give off from their axis-cylinder or nervous process numerous lateral processes, which end free in the grey matter. Most, or perhaps all, of the fibres in the anterior and lateral columns give off collateral fibres, which enter the grey matter, especially the anterior horns and the anterior part of the posterior cornu, where they end free. The longitudinal fibres of these two columns usually bend at a right angle and end free in the grey matter.

It is remarkable that all the collateral fibres and all the lateral branches of the nervous process of the nerve-cells, as well as those longitudinal fibres of the posterior, lateral, and anterior columns that enter the grey matter, break up into a greater or less number of branches, and end at last in a fine tuft of fibrils which surround the nerve-cells, without, however, forming connections with the nerve-cells or the fibrils anastomosing amongst themselves.]

[Three kinds of nerve-cells have been distinguished :—

(1) Large motor cells ; (2) cells which give nerve-fibres to the columns of the cord ; and (3) cells with a nervous process which does not pass out of the grey matter, but divides uniformly in the grey matter itself. The last variety of cell occurs only in the posterior cornu. The protoplasmic processes of all the nerve-cells branch and are continued sometimes as enormously long processes in all directions ; sometimes they pass into the white matter, but they never anastomose, and never give rise to a nerve-fibre (figs 551, 552).]

[The anterior commissure contains—

(1) Nervous processes from cells in all parts of the grey matter, and after they decussate are continued as longitudinal fibres of the antero-lateral columns.

(2) Decussating collateral fibres from the anterior and lateral columns.

(3) Decussating protoplasmic processes of some of the median cells of the anterior cornua.

The posterior commissure contains—

(1) Decussating collateral fibres of the posterior columns, and perhaps also from the posterior part of the lateral columns, as well as some decussating protoplasmic nervous processes from some of the cells of the posterior cornu and gelatinous substance.]

[The following fibres are directly connected with nerve-cells, and must be influenced by the latter:—

(1) The motor fibres in the anterior roots.

(2) Many fibres in the lateral and anterior columns.]

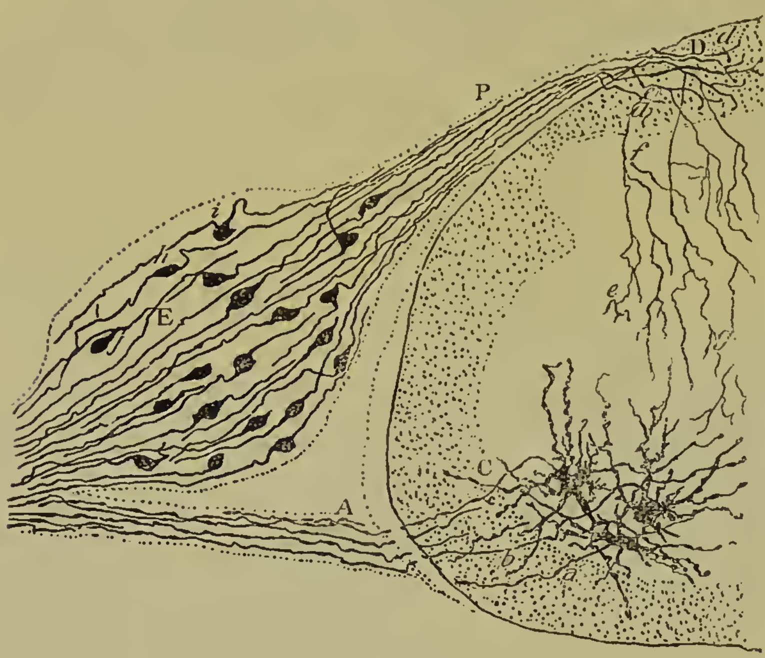


Fig. 552.

Transverse section of the spinal cord in the thoracic region in an embryo fowl (9th day of incubation). *A*, anterior, and *P*, posterior root ; *C*, axis-cylinder of a motor nerve-cell ; *D*, intra-medullary part of the posterior root ; *e*, origin of a collateral branch, which ramifies as *f g*, terminal ramifications of the collateral fibres ; *d*, final bifurcation ; *h*, bipolar ganglionic cells ; *i*, a unipolar nerve-cell like those in mammals (*Ramón y Cayal*).

[In the following instances, however, there is no direct continuity between fibres and cells, so that they can only act on each other by contact :—

(1) The sensory fibres that end free in the cord.

(2) The free terminations in the cord of the collateral fibres from all the columns.

(3) Many of the longitudinal fibres of the antero-lateral column, which bend round and end free in the grey matter.

(4) The free terminations of many lateral processes of the nervous or axis-cylinder process of many nerve-cells of the grey matter.

(5) The free terminations of the branched processes of certain cells of the posterior horn, that end *in toto* in the grey matter.]

[The glia-cells are developed from the elements of the original medullary plate, and are divided into primary and secondary. The former are represented by the epithelium lining the central canal. The others arise in the grey and white matter and appear to be epiblastic in origin.]

[The foregoing account represents Kölliker's *resumé* of his own researches on embryo mammals, which are practically a confirmation of the prior observations of Golgi and Ramón y Cayal, but more especially of the latter. It is obvious that the statements here made that the protoplasmic processes of nerve-cells do not anastomose, and that many white nerve-fibres terminate in the cord in free endings, without forming direct anatomical continuity with nerve-cells, must profoundly modify our conceptions and theories regarding the mode of action of these structures. It would seem that in certain cases an impulse reaching the grey matter through

such nerve-fibres must act on nerve-cells merely as the result of contact between the nerve-fibrils and the nerve-cell, and not in virtue of actual anatomical continuity.]

[**Functions of the Spinal Cord.**—(1) It is a great **conducting medium**, conducting impulses upwards and downwards, and within itself from side to side; (2) the great **reflex centre**, or rather series of so-called centres; (3) **impulses originate** within it, *i.e.*, its **automatic functions.**]

Conducting Systems.—The whole of the longitudinal fibres of the spinal cord may be arranged systematically in special bundles, according to their function.

[**Methods of ascertaining Conducting Paths in the Cord.**—The course of the fibres and their division into so-called systems has been ascertained partly by **anatomical** and **embryological**, partly by **physiological** and **pathological** means. Apart from experimental methods, such as dividing one column of the cord and observing the results, we have the following methods of investigation:—(1) Türck found that injury or disease of certain parts of the brain was followed by a degeneration downwards, or **secondary descending degeneration** of certain of the nerve-fibres connected with the seat of injury, *i.e.*, they were separated from their trophic centres and underwent degeneration. (2) P. Schiefferdecker found also, after section of the cord, that above the level of the section, certain definite tracts of white matter underwent degeneration [thus showing that certain tracts had their trophic centre below; this constitutes **secondary ascending degeneration**]. (3) **Gudden's Method.**—He showed, as regards the brain, that excision of a sense-organ in a young growing animal was followed by atrophy of the nerve-fibres and some other parts connected with it. Thus, the optic nerve and anterior corpora quadrigemina atrophy after excision of the eyeball in young rabbits.] (4) **Embryological.**—Flechsig showed that the fibres of the cord [and the brain also] during development became *covered with myelin* at different periods, those fibres becoming medullated latest which had the longest course. By a combination of these methods the following tracts of fibres have been mapped out:—

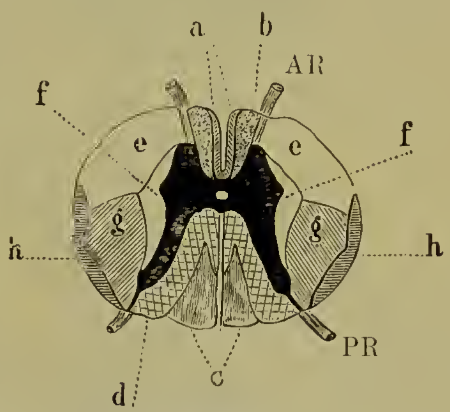


Fig. 553.

Scheme of the conducting paths in the spinal cord at the 3rd dorsal nerve. The black part is the grey matter. AR, anterior, PR, posterior, root; *a*, direct, and *g*, crossed, pyramidal tracts; *b*, anterior column ground bundle; *c*, Goll's column; *d*, postero-external; column; *e* and *f*, mixed lateral paths; *h*, direct cerebellar tracts.

Conducting Systems of Fibres.—1. In the **anterior column** lie (*a*) the uncrossed, anterior, or **direct pyramidal tract** [also called the **Column of Türck**]; and external to it is (*b*) the **anterior ground bundle**, or **anterior radicular zone** (fig. 553). [The direct pyramidal tract varies in size, and it generally extends downwards in the cord to about the middle of the dorsal region, diminishing steadily in its course. It is called direct pyramidal tract because, unlike the rest of the pyramidal tract, it does not decussate in the bulb. It is found only in man and the monkey, is very variable in size, and forms 10 to 20 per cent. of the total pyramidal tract. We do not know exactly how these fibres end, whether they cross to the opposite side, or remain on the same side, but most probably most of them pass through the anterior commissure to the grey matter of the opposite side.]

2. In the **posterior column** we distinguish (*c*) **Goll's column**, or the **postero-median** (postero-internal) **column**; and (*d*) the **outer root zone**, or the **funiculus**

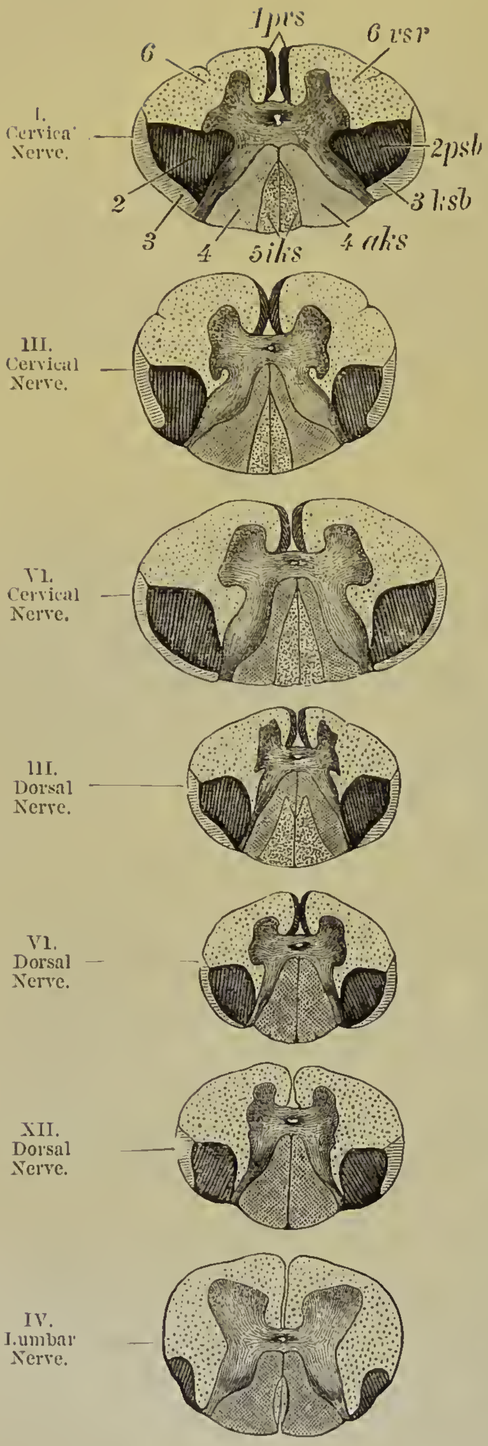


Fig. 554.

Scheme of the distribution of the chief paths in the spinal cord. 1 *pvs*, direct pyramidal tract; 2 *psb*, crossed pyramidal tracts; 3 *ksb*, direct cerebellar tract; 4 *aks*, postero-external column; 5 *iks*, postero-internal column, or Goll's column; 6 *vsr*, anterior mixed zone. × 2.

cuneatus, or *Burdach's column*, or the *posterior radicular zone*, or the *postero-external column* (figs. 553, 557).

3. In the **lateral column** are (*e*) the **antero-lateral tract** and (*f*) the **lateral mixed paths**, or *lateral limiting tract* [this tract is still further subdivided, p. 783], (*g*) the lateral or **crossed pyramidal tract**, and (*h*) the **direct cerebellar tract.**

[All the impulses from the central convolutions or motor areas of the cerebrum, by means of which **voluntary movements** (§ 365) are executed, are conducted by the **pyramidal tracts** (figs. 553 *a*, *g*, 554, 557). The fibres in these tracts descending from the central convolutions—*i.e.*, the motor-areas—pass through the white matter of the cerebrum, converging like the rays of a fan to the internal capsule, where they lie in the knee and anterior two-thirds of its posterior segment (the fibres for the face at the knee, and behind this in order those for the arm and leg), they then enter the middle-third of the crusta (fig. 628, *Py*), pass through the pons into the anterior pyramids of the medulla oblongata, where the great mass crosses over to the lateral column of the opposite side of the cord (**crossed pyramidal tract**), a small part descending in the cord on the same side as the **direct pyramidal tract**, *a*. The **crossed pyramidal tract** lies external to the posterior half of the grey matter in the lateral column (fig. 553, *g*), and it extends throughout the length of the cord. It contains nerve-fibres of all sizes. In the greater part of its course it is separated from the surface by the direct cerebellar tract, but where the latter lies further forward, as at the third cervical segment and lower dorsal region, its posterior surface reaches the surface, while from the last dorsal segment, throughout the lumbar region, it comes quite to the surface, as the direct cerebellar tract ceases at the first lumbar vertebra. The pyramidal tract diminishes from above downwards, and its fibres pass into the grey matter of the anterior cornu, and in all probability they subdivide to form fine fibrils, which come into relation with the dense thicket of fine fibrils produced by the subdivision of the processes of the multipolar nerve-cells. At least

they come into intimate relation—(direct union or contact?)—with the nervous mechanism in the anterior cornua of the grey matter of the cord. From each multipolar nerve-cell a nerve-fibre proceeds and passes into the anterior root. The facts connected with the descending degeneration of this tract seem to indicate that in the cord some of the fibres cross and descend in the opposite side of the cord. These are called the "**recrossed fibres**" (*Sherrington*). It would seem that the fibres of the direct pyramidal tract, as they descend in the cord, cross to the opposite side of the cord before they become continuous with the nerve-cells of the anterior cornu. They perhaps cross *viâ* the anterior white commissure.]

The **direct cerebellar tract** (figs. 553, 554, 557 *h*), begins about the first lumbar nerve, and increases in thickness from below upwards, but many of its fibres enter it at the first lumbar and lowest dorsal nerves. It is obvious, therefore, that the tract receives fibres as it passes upwards. It forms a thin layer on the surface of the cord. Its fibres, which are broad and coarse, very probably arise in the cells of Clarke's column (p. 769). As Clarke's column is connected with some of the fibres of the posterior root (for the trunk of the body), it follows that this tract connects certain parts of the posterior roots with the cerebellum. The fibres pass up through the cord and restiform body to the cerebellum. When it is divided, it degenerates upwards, so that it is supposed to conduct impulses in a centripetal direction. The degeneration, however, diminishes as we trace it upwards. This means that all the fibres do not necessarily ascend to the cerebellum. The tract receives new fibres as we trace it upwards, but some of the fibres pass to other parts of the cord as it is traced upwards, while others go direct to the cerebellum. Degeneration in it cannot be caused by injury or section of the nerves or nerve-roots, the cord itself must be injured, so that it is evident that the fibres of the tract do not come directly from the posterior root. Their **trophic centre** seems to be in Clarke's column (p. 769).]

The anterior (fig. 553, *e*) and lateral paths (*f*) and the anterior ground bundle (*b*) represent the channels which connect the grey matter of the spinal cord and that of the medulla oblongata; they represent the channels for reflex effects, and they also contain those fibres which are the direct continuation of the anterior spinal nerve-roots, which enter the cord at different levels and penetrate into the grey matter. In *e* and *f* there are some sensory paths. Lastly, *c* unites the posterior roots with the grey nuclei of the funiculi graciles of the medulla oblongata; *d* connects some of the posterior nerve-roots through the restiform body with the vermiform process of the cerebellum (*Flechsig*). The direction of conduction in the posterior columns, which are continuations of some of the fibres of the posterior roots, is upwards, as part of them degenerates upwards after section of the posterior root. Of the fibres of each posterior root, some pass directly into the posterior horn, another part ascends in the posterior column of the same side, and gradually as it ascends it comes nearer the posterior median fissure. Some of these fibres enter the grey matter of the posterior horn at a higher level. The fibres of the posterior columns run upwards as far as the interolivary layer and the decussation of the pyramids, where they seem to end, or at least form connections with the nerve-cells of the funiculi graciles [clava] and cuneati [triangular nucleus]. A small part as arcuate fibres join the restiform body, and thus the cerebellum is connected with the posterior columns.

Further, the transverse **sectional area** of the direct and crossed pyramidal tracts (fig. 554), the lateral cerebellar tract, and Goll's column gradually diminish from above downwards; they serve to connect intracranial central parts with the ganglionic centres distributed along the spinal cord. The anterior root bundle, the funiculus cuneatus, and the anterior mixed lateral tracts vary in diameter at different parts of the cord, corresponding to the number of nerve-roots. It has been concluded from this that these tracts serve to connect the grey matter at

different levels in the cord with each other, and ultimately with the medulla oblongata, so that they do not pass directly to the higher parts of the brain (fig. 536).

Trophic Centres of the Conducting Paths.—Türck observed that the destruction of certain parts of the brain caused a **secondary degeneration** of certain parts of the cord, corresponding to the parts called *pyramidal tracts* by Flechsig (fig. 554). P. Schieferdecker found the same effects *below* where he divided the spinal cord in a dog. Hence it is concluded that the *nutritive* or *trophic centre* of the pyramidal tracts lies in the cerebrum. [Section of the cord, or an injury compressing the cord, besides giving rise to loss of certain functions (p. 796), results in structural changes in certain limited areas of the cord itself.]

[All that is meant by the terms descending and ascending degeneration is, that after section or injury of the cord, or certain parts of the brain, definite areas of the white matter of the cord above and below the seat of the lesion undergo degeneration. It does not mean that the degeneration proceeds at a given rate upwards or downwards from the seat of the lesion, for it appears that the degeneration may be quite as far advanced at a distance from the lesion as near it, so that, perhaps, the degenerations in the cord are not exactly identical with those that occur in a nerve after it is divided. In the cord the axis-cylinders break up and are absorbed, and we know that in the cord nerve-fibres have no primitive sheath, and there are no nuclei, *i.e.*, nerve-corpuscles, to proliferate, as is the case in the Wallerian degeneration of a nerve.]

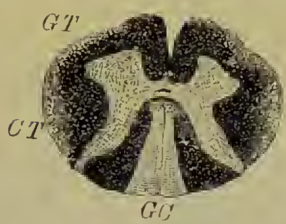


Fig. 555.

Fig. 556.

Fig. 555.—Ascending degeneration in the cervical enlargement. G C, Goll's column, degenerated on both sides, and to a less degree the cerebellar tract, C T, and Gower's tract, G T. × 2. Fig. 556.—Descending degeneration after a lesion on the left side of the brain. The anterior pyramidal tract of the left side and the crossed pyramidal tract of the opposite side are degenerated. × 2.

[The tracts which in each half of the cord undergo **descending degeneration** are (figs. 555, 557):—

1. The crossed pyramidal tract.
2. The direct pyramidal tract.
3. The antero-lateral descending tract.
4. The descending comma tract.

The tracts undergoing **ascending degeneration** are (figs. 556, 557):—

1. Goll's column or posterior-median tract.
2. The cerebellar tract.
3. The ascending antero-lateral tract or tract of Gowers.]

Below the section, after a time, the **direct** and **crossed pyramidal tracts** (figs. 557, 558, 1, 1′, 2, 2′) degenerate *downwards, i.e.*, they undergo **descending degeneration**, because they are cut off from their nutritive or trophic centres, which are situated above in the pyramidal cells of the motor areas of the brain (§ 378). [It is important to note that almost all the fibres in these tracts degenerate, so that these tracts are sharply defined after they have degenerated.] The trophic centres for the fibres of the anterior root lies in the multipolar nerve-cells of the anterior cornu of the grey matter of the cord.

[These are the most conspicuous descending tracts, but there is also a very diffuse area, some of the fibres only in which undergo descending degeneration. It lies in the antero-lateral column, and is called the **antero-lateral descending tract.** It stretches as a somewhat narrow curved area from the crossed pyramidal tract towards the anterior column (fig. 557), and internal to the ascending tract of the

same name. Only a limited number of the fibres in this area degenerate, many remaining unchanged. The small narrow **descending comma tract** (fig. 557), which lies in the postero-external column, can hardly be called a tract, as it does not extend along the length of the cord after section of the latter; in fact, it only extends a short distance, and it may represent some fibres of the posterior root which take a descending course after entering the cord.]

[**Ascending Tracts.**—After section of the spinal cord, Goll's column and the direct cerebellar tracts and the tract of Gowers degenerate *upwards, i.e.,* they undergo **ascending degeneration.** If the posterior columns even be divided, **Goll's column** or the **postero-median column** degenerates upwards towards the medulla oblongata, and the degeneration ends in the posterior pyramidal nucleus or clava. Goll's column extends along the whole length of the cord, varying, however, in size at different levels. It consists of small fibres of a nearly uniform size

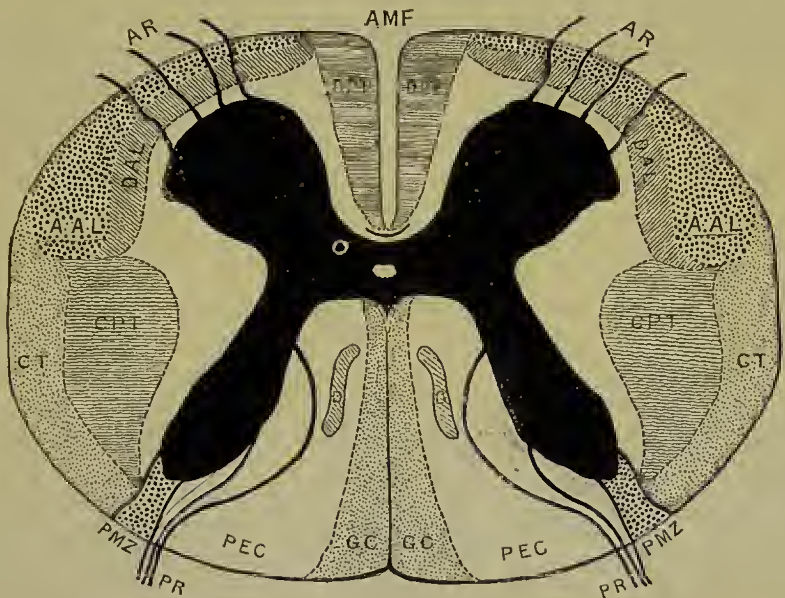


Fig. 557.

Scheme showing the degeneration tracts, and the paths that do not undergo degeneration in the cord. AMF, anterior median fissure; DPT and CPT, direct and crossed pyramidal tracts; AR and PR, anterior and posterior roots; AAL and DAL, ascending and descending antero-lateral tracts; CT, cerebellar tract; D, comma-shaped tract; PMZ, posterior marginal zone; PEC, postero-external column. The parts left white do not undergo degeneration.

(fig. 556). The same result occurs if the posterior nerve-roots of the cauda equina, or other posterior nerve-roots, be injured. Hence fibres seem to pass from the posterior root into these columns, and the nerve-cells in the clava must also have an important relation to these nerve-fibres and the parts whence they are derived. The postero-external column remains undegenerated, so that there is a very sharp distinction between the two parts of the posterior column. As Goll's column degenerates upwards, it points to its fibres conducting impulses in a centripetal direction, and to the nutritive centre for its nerve-fibres being below. The trophic centre is probably in the spinal ganglion of the posterior root.]

[It is a most important fact that ascending degeneration occurs in Goll's column after section of the posterior roots of any of the spinal nerves. Suppose the lower two or three dorsal posterior roots to be divided, the degeneration proceeds centripetally along the nerve-roots to the cord, and can be traced into the postero-external column for a short distance upward in this column—as the zone

of Lissauer—but at a certain distance above the entrance of the nerve-roots no degeneration is found in the postero-external column, while now the degenerated fibres can be traced in the postero-internal or Goll's column, and some of the degenerated fibres—not all—can be traced up to the bulb. The degeneration is confined to the side in which the nerve-roots are divided. This means that fibres of the posterior root enter the cord, run for a short distance in the postero-external zone, and in Lissauer's zone; they then enter Goll's column, and some of them pass up to the bulb, while others enter the grey matter to form connections with its nerve-cells. The fibres proceeding from the several posterior nerve-roots, and which pass through Goll's column to the bulb, occupy a definite position in this column. Those fibres which arise from the sacral nerves lie near the middle line dorsally, while those from the lumbar region lie near the middle line, but are placed ventrally, while those from the dorsal region are in front of the lumbar area and extend laterally, and are nearer the commissure of the cord.]

[The **direct cerebellar tract** (fig. 557), also an elongated curved tract of fibres lying in the dorsal part of the cord and superficial to the crossed pyramidal tract, also undergoes ascending degeneration if the cord be divided at any level above the junction of the dorsal and lumbar region. This tract appears to begin in the upper lumbar region, about the level of the first lumbar nerve, and it appears to be absent in the lower lumbar and sacral regions. At least, section of the cord in these regions is not followed by degeneration in the cerebellar tract. The tract increases in size from below upwards, and the degeneration can be traced through the restiform body into the cerebellum. The fibres composing this tract are mostly all large, coarse, or broad fibres, and it is suggested that their trophic centre lies in the cells of Clarke's column (p. 769). It is important to note that degeneration of this tract follows only when the cord itself is divided, and not when the posterior nerve-roots are cut.]

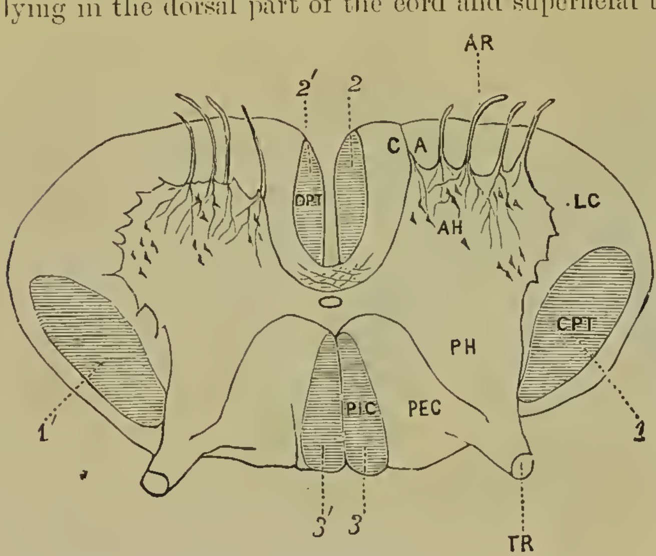


Fig. 558.

Transverse section of the spinal cord, showing some of the secondary degeneration tracts. AR, anterior, TR, posterior root; 1, 1′ (CPT), region of the crossed pyramidal tract; 2 2′ (DPT) PEC, postero-external column; LC, lateral column.

[The **ascending antero-lateral tract** or **tract of Gowers** also undergoes ascending degeneration, but only after injury of the cord, not of the nerve-roots (figs. 557, 556). It lies superficially on the anterior aspect of the lateral column (fig. 557), and extends along the whole length of the cord. It fills up the area superficial to the crossed pyramidal, cerebellar, and descending antero-lateral tracts. All the fibres in this area do not degenerate. The degenerate ones are always intermixed with a considerable number of normal fibres. The nerve-fibres which compose this tract are intermediate in size between the large fibres of the cerebellar tracts and the fine fibres of Goll's column. By some it is said to pass to the cerebellum, and to be merely an outlying part of the cerebellar tract. Its fibres are perhaps derived from certain cells in the grey matter of the cord in which some of the fibres of the posterior root terminate.]

[**Areas which do not degenerate.**—Even when we have accounted for the foregoing fibres, there still remains considerable areas of fibres which do not undergo degeneration either after section, injury, or disease of the cord. This area includes the anterior ground bundle or antero-external column, the postero-external column, and a considerable part of the lateral column, forming an elongated area bounding the grey matter of its own half of the cord. It has been suggested that those **fibres** of the spinal cord which **do not degenerate** after section of the cord are commissural in function, connecting ganglionic cells with each other, and are, therefore, provided with a trophic centre at both ends. Of the above-named areas, the postero-external column is composed chiefly of fibres of the posterior root.]

To the posterior root also belongs a very small area of fibres lying on the posterior aspect of the tip of the posterior horn, and known as the **posterior marginal zone** or **zone of Lissauer**, which is composed of very fine fibres (fig. 557).]

Time of Development of the Spinal Tracts.—With regard to the time of development of the individual systems, Flechsig finds that the first-formed paths are those between the periphery and the central grey matter, especially the *nerve-roots*, *i.e.*, they are the first to be covered with the myelin. Then fibres which connect the grey matter at different levels are formed—the fibres which connect the grey matter of the cord with the cerebellum, and also the former with the tegmentum of the cerebral peduncle. At last the fibres which connect the ganglia of the pedunculus cerebri, and perhaps also the grey matter of the cortex cerebri with the grey matter of the cord are formed. In cases of anencephalous fœtuses, *i.e.*, where the cerebrum is absent, neither the pyramidal tracts nor the pyramids are developed. In the *brain* before birth, medullated nerve-fibres are formed in the paracentral, central, and occipital convolutions, and in the island of Reil, and last of all in the frontal convolutions (*Tuczek*). [At birth, all the tracts of the cord are medullated except the pyramidal tracts, so that in a section of the cord of a new-born child these tracts appear grey in the contrast to the other white tracts of the cord.]

360. SPINAL REFLEXES.—By the term **reflex movement** is meant a movement caused by the stimulation of an *afferent* (sensory) nerve. The stimulus, on being applied to an **afferent nerve**, sets up a state of excitement (nervous impulse) in that nerve, which state of excitement is transmitted or conducted in a *centripetal* direction along the nerve to the *centre* (spinal cord in this case); where the nerve-cells represent the **nerve-centre** in the cord, the impulse is transferred to the motor, **efferent** or *centrifugal* channel. **Three factors**, therefore, are essential for a reflex motor act—a centripetal or **afferent fibre**, a transferring **centre**, a centrifugal or **efferent fibre**; these together constitute a **reflex arc** (fig. 559). In a purely reflex act all voluntary activity is excluded.

Reflex movements may be divided into the three following groups :—

I. The **simple** or **partial reflexes**, which are characterised by the fact that stimulation of a sensory area discharges movement in one muscle only, or at least in one limited group of muscles. **Example** :—Contact with the conjunctiva causes closure of the eyelids; the afferent nerve is the 5th and the efferent the 7th cranial nerve, and the centre lies in the grey matter of the medulla oblongata.

II. **The extensive inco-ordinate reflexes**, or **reflex spasms.**—These movements occur in the form of clonic or tetanic contractions; individual groups of muscles, or all the muscles of the body may be implicated. **Causes** :—A reflex spasm depends upon a double cause—(*a*) Either the grey matter or the spinal cord is in a condition of *exalted excitability*, so that the nervous impulse, after having reached the centre, is easily transferred to the neighbouring centres. This excessive excitability is produced by certain poisons, more especially by *strychnin*, brucia, caffein, atropin, nicotin, carbolic acid, &c. The slightest touch applied to an animal poisoned with strychnin is sufficient to throw the animal at once into spasms. Pathological conditions may cause a similar result: thus, there is excessive excitability in hydrophobia and tetanus. On the other hand, the central organ may be in such a condition that extensive reflexes cannot take place; thus, in the condition of apnœa, the spasms that occur in poisoning with strychnin do not take

place (*J. Rosenthal and Leube*); this is brought about by the passive artificial respiratory movements stretching the cutaneous nerves of the chest and abdomen (§ 361, 3). The performance of other passive periodic movements in various parts

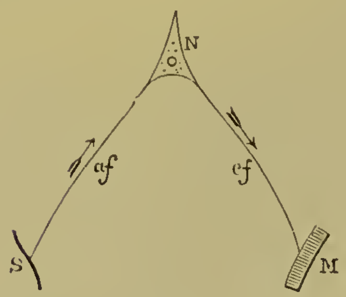


Fig. 559.

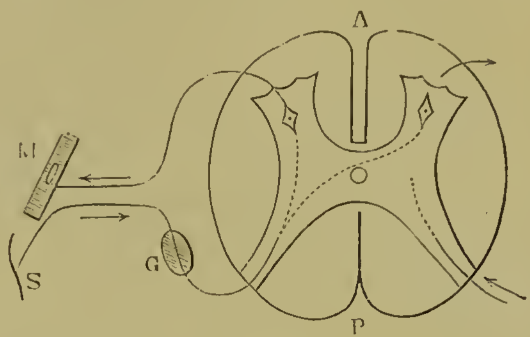


Fig. 560.

Fig. 559.—Scheme of a reflex arc. S, skin; M, muscle; N, nerve-cell, with *af*, afferent, and *ef*, efferent fibres. Fig. 560.—Section of a spinal segment, showing a unilateral and crossed reflex act. A, anterior, and P, posterior surface; M, muscle; S, skin; G, ganglion.

of the body also produces a similar condition (*Buchheim*). If the spinal cord be cooled very considerably, reflex spasms may not occur (*Kunde*). (*b*) Extensive reflex movements may also take place when the discharging *stimulus is very strong*. **Examples** of this condition occur in man, thus—intense neuralgia may be accompanied by extensive spasmodic movements.

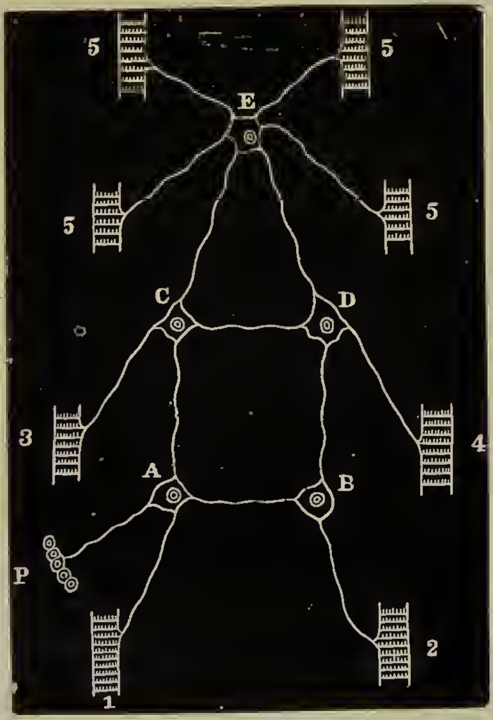


Fig. 561.

Scheme of mode of propagation of reflex movements. P, skin; A, B, C, D, motor cells in spinal cord; 1, 2, 3, 4, 5, muscles. (In the light of the recent results of Golgi and Cayal, the scheme is no longer valid.)

[Fig. 561 shows the mechanism of simple and complex reflex movements. Suppose the skin to be stimulated at P, an impulse is sent to A and from it to a muscle 1 on the same side, resulting in a **unilateral** simple reflex movement—the resistance being less in this direction than in the other channels. If the impulse be stronger, or the transverse resistance in the cord diminished, the impulse may pass to B, thence to 2, resulting in a **symmetrical** reflex movement on both sides. But if a very strong impulse reach the cord, or if the excitability of the grey matter be increased, *e.g.*, by strychnin, the resistance to the diffusion of the impulse is diminished, and it passes upward to C and D, resulting in more complex movements—thus there is **irradiation**—or it may even affect the centres in the medulla oblongata, E, giving rise to general convulsive movements.]

General spasms usually manifest themselves as "**extensor tetanus**" or "**opisthotonus**," because the extensors overcome the flexor muscles. Nerves which arise from the medulla oblongata may be excited through the stimulation of distant afferent nerves, without general spasms being produced.

Strychnin is the most powerful reflex-producing poison we possess, and it acts upon the grey matter of the spinal cord. [An animal poisoned with strychnin exhibits tetanic spasms on the application of the slightest stimulus. All the muscles become rigid, but the extensors overcome the flexors.] If the heart of a frog be ligatured, and the poison afterwards applied directly to the spinal cord, reflex spasms are produced, proving that strychnin acts upon the spinal cord. During the spasm the heart is arrested in diastole, owing to the stimulation of the vagus,

while the arterial blood-pressure is greatly increased owing to stimulation of the central vaso-motor centres of the medulla oblongata and spinal cord. Mammals may die from asphyxia during the attack; and after large doses, death may occur, owing to paralysis of the spinal cord, due to the frequently recurring spasms. Fowls are unaffected by comparatively large doses. [We can prove that strychnin does not produce spasms by acting on the brain, muscle, or nerve. Destroy the brain of a frog, divide one sciatic nerve high up, and inject a small dose of strychnin into the dorsal lymph-sac; in a few minutes all the muscles of the body, except those supplied by the divided nerve, will be in spasms, showing that although the poisoned blood has circulated in the nerves and muscles of the leg, it does not act on them. Destroy the spinal cord, and the spasms cease at once.]

Summation of Stimuli.—By this term is meant that a single weak stimulus, which in itself is incapable of discharging a reflex act, may, if repeated sufficiently often, produce this act. The single impulses are conducted to the spinal cord, in which the process of "summation" takes place. According to J. Rosenthal, 3 feeble stimuli per second are capable of producing this effect, although 16 stimuli per second are most effective. On increasing the number of stimuli per second, no further increase of the reflex act is possible. Other observers (*Stirling*, *Ward*) have found that stimuli, such as induction shocks, are active within much wider limits, *e.g.*, from 0·05 to 0·4 second interval. W. Stirling has shown it to be extremely probable that all reflex acts are due to the repetition of impulses in the nerve-centres.

[Strychnin interferes with the summation of stimuli, but the reflex excitability is so greatly exalted that a minimal stimulus is at the same time a maximal one.]

Pflüger's Law of Reflex Actions.—(1) The reflex movement occurs on *the same side* on which the sensory nerve is stimulated; while only those muscles contract whose nerves arise from the same segment of the spinal cord. (2) If the reflex occur on the *other* side, only the corresponding muscles contract. (3) If the contractions be unequal upon the two sides, then the most vigorous contractions always occur on the side which is stimulated. (4) If the reflex excitement extend to other motor nerves, those nerves are always affected which lie in the direction of the medulla oblongata. Lastly, all the muscles of the body may be thrown into contraction.

Crossed Reflexes.—There are exceptions to these rules. If the region of the eye be irritated in a frog whose cerebrum is removed, there is frequently a reflex contraction in the hind limb of the opposite side (*Luchsinger*, *Langendorff*). In beheaded tritons and tortoises, and in deeply narcotised dogs and cats, tickling one fore limb is frequently followed by a movement of the hind limb of the opposite side (*Luchsinger*). This phenomenon is called a "**crossed reflex**" (fig. 560). If the spinal cord be divided along the middle line throughout its entire extent, then of course the reflexes are confined to *one side* only (*Schiff*).

III.—Extensive co-ordinated reflexes are due to stimulation of a sensory nerve, causing the discharge of complicated reflex movements in whole groups of different muscles, the movements being "**purposive**" in character, *i.e.*, as if they were intended for a particular purpose.

Methods.—The experiments are made upon *cold-blooded animals* (decapitated or pithed frogs, tortoises, or eels) or upon *mammals*. In the latter, artificial respiration is kept up, and the four arteries going to the head are ligatured, in order to eliminate the action of the brain (*Sig. Mayer*, *Luchsinger*). The reflexes of the lower part of the spinal cord may be studied on animals (or men), in cases where the spinal cord is divided transversely in the upper dorsal region. In such cases some time must elapse in order that the primary effect of the lesion (the so-called shock), which usually causes a diminution of the reflexes, may pass off. Very young mammals exhibit reflexes for a considerable time after they are beheaded.

Examples:—1. The **protective movements** of pithed or decapitated frogs. [If a drop of a dilute acid be applied to the skin of such a frog, immediately it strives to get rid of the offending body, and it generally succeeds in doing so.] Similarly, it kicks against any fixed body pushed against it. These movements are so purposive in their character, and the actions of groups of muscles are so adjusted to perform a particular act, that Pflüger regarded them as directed by and due to "consciousness of the spinal cord." If a flame be applied to the side or part of the body of an eel, the body is moved away from the flame. The tail of a decapitated

triton, tortoise, newt, eel, or snake is directed towards a gentle stimulus, but if a violent stimulus is used, it is directed away from it (*Luchsinger*).

2. **Goltz's Croaking Experiment.**—A pithed (male) frog, *i.e.*, one with its cerebral lobes alone removed (or one with its eyes or ears destroyed—*Langendorff*), croaks every time the skin of its back or flanks is gently stroked. [Some male frogs, when held up by the finger and thumb immediately behind the fore legs, croak every time gentle pressure is made on their flank.]

3. **Goltz's "Embrace Experiment."**—During the breeding season in spring, the part of the body of the male frog between the skull and the fourth vertebra embraces every rigid object, which is brought into contact with, and gently stimulates, the skin over the sternum.

In the *intact* animal, the exciting stimulus lies in the degree of filling of the male seminal organ (*Tarchanoff*). The reflex ceases at once on gently stimulating the optic lobes (*Albertoni*).

4. In **mammals** (dogs), the following reflex acts are performed by the posterior part of the spinal cord, even after it is separated from the rest of the cord:—[In mammals, however, the cord takes a long time to recover from the shock of the operation, compared with the time required for this result in cold-blooded animals.] Scratching with the hind feet a part of the skin which has been tickled (just as in intact animals); the movements necessary for emptying the bladder and for defæcation, as well as those necessary for erection; the movements necessary for parturition (*Goltz*, *Freusberg and Gergens*). Co-ordinated movements do not, as a rule, occur simultaneously in portions of the spinal cord lying widely apart after removal of the medulla oblongata. According to Ludwig and Owsjannikow, the medulla oblongata perhaps contains a reflex organ of a higher order, which forms, as it were, a centre for combining, through the medium of the nerve-fibres, the various reflex provinces in the spinal cord.

5. Co-ordinated reflexes may occur in man during **sleep**, and during pathological comatose conditions.

Most of the movements which we perform while we are awake, and which we execute **unconsciously**—or even when our psychical activities are concentrated upon some other object—really belong to the category of co-ordinated reflexes. Many complicated motor acts must first be learned—*e.g.*, dancing, skating, riding, walking—before unconscious harmonious co-ordinated reflexes can again be discharged. The co-ordinated reflex movements of coughing, sneezing, and vomiting depend upon the spinal cord, together with the medulla oblongata.

The following facts are also important:—

1. Reflexes are more easily and more completely discharged when the **specific end-organ** of the afferent nerve is stimulated, than when the trunk of the nerve is stimulated in its course (*Marshall Hall*, 1837). [Thus, by gently tickling the skin, it is easy to discharge a reflex act, while it requires a strong stimulus to be applied to an exposed sensory nerve in order to do so.]

2. A *stronger stimulus* is required to discharge a reflex movement than for the direct stimulation of motor nerves.

3. A movement produced reflexly is of *shorter duration* than the corresponding movement executed voluntarily. Further, the occurrence of the movement after the moment of stimulation is *distinctly delayed.* In the frog, a period nearly twelve times as long elapses before the occurrence of the contraction than is occupied in the transmission of the impulse in the sensory and motor nerves (*Helmholtz*, 1854). Thus, the spinal cord offers *resistance* to the transmission of impulses through it.

The term "**reflex time**" is applied to the time necessary in the cord itself for transferring the impulse from the afferent fibre to the nerve-cells of the cord, and from them to the efferent fibre. In the frog it is equal to 0·008 to 0·015 second. The time, however, is increased by almost one-third, if the impulse pass to the *other* side of the cord, or if it pass along the cord, *e.g.*, from the sensory nerves of the anterior extremity to the motor roots of the posterior limb. Heat diminishes the reflex time and increases the reflex excitability. Lowering the temperature

(winter frogs), as well as the reflex-exciting poisons already mentioned, *lengthens the reflex time*, whilst the reflex excitability is simultaneously increased. Conversely, the reflex time diminishes as the strength of the stimulus increases, and it may even become of minimal duration (*J. Rosenthal*). The reflex time is determined by ascertaining the moment at which the sensory nerve is stimulated, and the subsequent contraction occurs. Deduct from this the time of latent stimulation (§ 298, I.), and the time necessary for the conduction of the impulse (§ 298) in the afferent and efferent nerves (*v. Helmholtz, J. Rosenthal, Exner, Wundt*).

[**Influence of Drugs.**—The latent period and reflex time are influenced by a large number of conditions. In a research, still unpublished, W. Stirling finds that the latent period may remain nearly constant in a pithed frog for nearly two days, when tested by Türck's method. Sodic chloride does not influence the time, nor does sodic bromide or iodide. Potassic chloride, however, lengthens it enormously, or even abolishes reflex action after a very short time, and so do potassic bromide, ammonium chloride and bromide, chloral and croton-chloral. The lithia salts also lengthen the reflex time, or abolish the reflex act after a time.]

361. INHIBITION OF THE REFLEXES.—Within the body there are mechanisms which can *suppress* or *inhibit* the discharge of reflexes, and they may therefore be termed **mechanisms inhibiting** the **reflexes**. These are :—

1. **Voluntary Inhibition.**—Reflexes may be inhibited voluntarily, both in the region of the spinal cord and brain. **Examples**:—Keeping the eyelids open when the eyeball is touched; arrest of movement when the skin is tickled. We must observe, however, that the suppression of reflexes is possible only up to a certain point. If the stimulus be strong, and repeated with sufficient frequency, the reflex impulse ultimately overcomes the voluntary effort. It is impossible to suppress those reflex movements which cannot at any time be performed voluntarily. Thus, erection, ejaculation, parturition, and the movements of the iris, are neither direct voluntary acts, nor can they, when they are excited reflexly, be suppressed by the will.

2. **Setschenow's inhibitory centre** is another cerebral apparatus, which in the **frog** is placed in the **optic lobes**. If the optic lobes be separated from the rest of the brain and spinal cord, by a section made below it, the reflex excitability is increased. If the lower divided surface of the optic lobes be stimulated with a crystal of common salt or blood, the reflex movements are suppressed. The same results obtain when only *one* side is operated on. Similar organs are supposed to be present in the corpora quadrigemina and medulla oblongata of the higher vertebrates. From 1 and 2 we may explain why reflex movements occur more regularly and more readily after separation of the brain from the spinal cord.

[**Quinine** greatly diminishes the reflex excitability in the frog, but if the medulla oblongata be divided, the reflex excitability of the cord is restored. The depression is ascribed by Chaperon to the action of the quinine on Setschenow's centres.]

3. **Strong stimulation of a sensory nerve** inhibits reflex movements. The reflex does not take place if an afferent nerve be stimulated very powerfully (*Goltz, Lewisson*). **Examples** :—Suppressing a sneeze by friction of the nose, [compressing the skin of the nose over the exit of the nasal nerve]; suppression of the movements produced by tickling, by biting the tongue. Very violent stimulation may even suppress the co-ordinated reflex movements usually controlled by voluntary impulses. Violent pain of the abdominal organs (intestine, uterus, kidneys, bladder, or liver) may prevent a person from walking or even from standing. To the same category belongs the fact that persons fall down when internal organs richly supplied with nerves are injured, there being neither injury of the motor nerves nor loss of blood to account for the phenomenon. Excitement of the central organs through other centripetal channels (nerves of special sense, and those of the generative organs) diminishes the reflexes in other channels.

4. It is important to note that in the suppression of reflexes, **antagonistic muscles** are often thrown into action, whether voluntarily or by the stimulation of sensory nerves, *i.e.*, reflexly. In some cases, in order to cause suppression of the reflex, it appears to be sufficient to direct our attention to the execution of such a complicated reflex act. Thus, some persons cannot sneeze

when they think intently upon this act itself (*Darwin*). The voluntary impulse rapidly reaches the reflex centre, and begins to influence it so that the normal course of the reflex stimulation, due to an impulse from the periphery, is interfered with (*Schlösser*).

5. **Drugs.**—Chloroform diminishes the reflex excitability by acting upon the centre, and a similar effect is produced by picrotoxin, morphia, narcotin, thebain, aconitin, quinine, hydrocyanic acid. [Chloroform may abolish the reflexes without arresting conduction. W. Stirling finds that chloral, potassic bromide and chloride, ammonium chloride, but not sodium chloride, greatly diminish the reflex excitability. Nicotin increases it in frogs (*Freusberg*).]

A **constant current** of electricity passed longitudinally through the cord diminishes the reflexes (*Ranke*), especially if the direction of the current is from above downwards (*Legros and Onimus, Uspensky*).

[Some **drugs** affect the reflex excitability **directly** by acting on the spinal cord, *e.g.*, methylconine, but other drugs may produce the same result **indirectly** by affecting the heart and the blood-supply to the cord. If the abdominal aorta of a rabbit be compressed for a few minutes to cut off the supply of blood to the cord and lower limbs, temporary paraplegia is produced.]

If frogs be asphyxiated in air deprived of all its O, the brain and spinal cord become completely unexcitable, and can no longer discharge reflex acts. The motor nerves and the muscles, however, suffer very little, and may retain their excitability for many days (*Aubert*).

[**Nature of Inhibition.**—The foregoing view assumes the existence of inhibitory centres, but it is important to point out that it has been attempted to explain this phenomenon without postulating the existence of inhibitory centres. During inhibition the function of an organ is restrained—during paralysis it is abolished, so that there is a sharp distinction between the two conditions. The analogy between inhibitory phenomena and the effects of interference of waves of light or sound has been pointed out by Bernard and Romanes, while Lauder Brunton has tried to explain the question on a physical basis, indicating that inhibition is not dependent on the existence of special inhibitory centres, but that stimulation and inhibition are different phases of excitement, the two terms being relative conditions depending on the length of the path along which the impulse has to travel, and the rate of its transmission. Brunton points out that the known facts are most consistent with an hypothesis of the interference of waves, one with another, than with the supposition that there are inhibitory centres for every so-called inhibitory act in the body. In discussing this question great regard must be had to the action of the vagus on the heart (§ 369).]

Türck's method of testing the reflex excitability of a frog is the following:—A frog is pithed, and after it has recovered from the shock its foot is dipped into *dilute sulphuric acid* [2 per 1000]. The time which elapses between the leg being dipped in and the moment it is withdrawn is noted. [The time may be estimated by means of a metronome, or the movements may be inscribed upon a recording surface. The time which elapses is known as the "period of latent stimulation."]

This time is greatly prolonged after the optic lobes have been stimulated with a crystal of common salt or blood, or after the stimulation of a sensory nerve.

Setschenow distinguished **tactile** reflexes, which are discharged by stimulation of the *nerves of touch*; and **pathic**, which are due to stimulation of *sensory* (pain-conducting) fibres. He and Paschutin suppose that the tactile reflexes are suppressed by voluntary impulses, and the pathic by the centre in the optic lobes.

Theory of Reflex Movements.—The following theory has been propounded to account for the phenomena already described:—It is assumed that the *afferent* fibre within the grey matter of the spinal cord joins one or more nerve-cells, and thus is placed in communication in all directions with the network of fibres in the grey substance. Any impulse reaching the grey matter of the cord has to overcome considerable **resistance**. The least resistance lies in the direction of those *efferent* fibres which emerge in the same place and upon the same side as the entering fibre. Thus, the feeblest stimulus gives rise to a *simple reflex*, which generally is merely a simple protective movement for the part of the skin which is stimulated. Still greater resistance is opposed in the direction of other motor ganglia. If the reflex impulse is to pass to these ganglia, either the discharging *stimulus* must be considerably *increased*, or the *resistance* within the connections of the ganglia of the grey matter must be *diminished*. The latter condition is produced by the action of the above-named poisons as well as during general increased nervous excitability (hysteria, nervousness). Thus, extensive reflex spasms may be produced either by increasing the stimulus, or by diminishing the resistance to conduction in the spinal cord. Those conditions which render the occurrence of reflexes more difficult, or

abolish them altogether, must be regarded as increasing the resistance in the reflex arc in the cord. The action of the reflex inhibitory mechanism may be viewed in a similar manner.

The fibres of the reflex arc must have a connection with the reflex inhibitory paths; we must assume that equally by the reflex inhibitory stimulation resistance is introduced into the reflex arc. The explanation of *extensive co-ordinated movements* is accompanied with difficulties. It is assumed that by use and also by heredity those ganglionic cells which are the first to receive the impulse are placed in the path of least resistance in connection with those cells which transfer the impulse to the groups of muscles, whose contraction, resulting in a co-ordinated purposive movement, prevents the body or the limb from being affected by any injurious influences.

[In the light of the recent results of Ramón y Cayal (p. 775), viz., that the afferent fibres break up in the grey matter of the cord, and terminate in fibrils which end free and do not anastomose with the processes of nerve-cells, we must assume that contact of fibrils is sufficient to enable impulses to be communicated from one fibril to another.]

Pathological.—Anomalies of reflex activity afford an important field to the physician in the investigation of nervous diseases. **Enfeeblement**, or even complete **abolition** of the reflexes may occur:—(1) Owing to diminished sensibility or complete insensibility of the afferent fibres; (2) in analogous affections of the central organ; (3) or, lastly, of the efferent fibres. Where there is general depression of the nervous activity (as after shocks, compression or inflammation of the central nervous organs; in asphyxia, in deep coma, and in consequence of the action of many poisons), the reflexes may be greatly diminished or even abolished.

[**Reflexes.**—The physician, by studying the condition of the reflexes, can form an idea as to the condition of practically every inch of the spinal cord. There are three groups of reflexes, (*a*) the **superficial**, (*b*) the **deep** or tendon, (*c*) the **organic reflexes.**]

[The **superficial cutaneous** or **skin reflexes** are excited by stimulating the skin, *e.g.*, by tickling, pricking, scratching, &c. We can obtain a series of reflexes from below as far up as the lower part of the cervical region. The **plantar reflex** is obtained by tickling the soles of the feet, when the leg on that side, or, it may be, both legs are drawn up. It is always present in health, and its centre is in the lumbar enlargement of the cord. The **cremasteric** reflex is well marked in boys, and is easily produced by exciting the skin on the inner side of the thigh, when the testicle on that side is retracted. The **gluteal** reflex consists in a contraction of the gluteal muscles, when the skin over the buttock is stimulated. The **abdominal** reflex consists in a similar contraction of the abdominal muscles, when the skin over the abdomen in the mammary line is stimulated. The **epigastric** reflex is obtained by stimulating the skin in front between the fourth and sixth ribs. The **interscapular** reflex results in a contraction of the muscles attached to the scapula, when the skin between the scapulæ is stimulated. Its centre corresponds to the lower cervical and upper dorsal region.]

[The following table, after Gowers, shows the relation of each reflex to the spinal segment or segments on which it depends:—

Cervical,	6	Interscapular (C. 6 – D. 1).	Lumbar,	1	Cremasteric (L. 1, 2).	
,,	7		,,	2	*Knee-jerk* (L. 2, 3).	
,,	8		,,	3		
Dorsal,	1		,,	4	Gluteal (L. 4, 5).	
,,	5	Epigastric (D. 5–7).	,,	5		
,,	6		Sacral,	1	*Ankle Clonus* (S. 1–3).	Plantar.
,,	7		,,	2		Vesical.
,,	8	Abdominal (D. 8–12).	,,	3		Rectal.
,,	9		,,	4		Sexual.]
,,	10		,,	5		
,,	11					
,,	12					

Another important diagnostic reflex is the "**abdominal reflex,**" which consists in this, that when the skin of the abdomen is stroked, *e.g.*, with the handle of a percussion-hammer, the abdominal muscles contract. When this reflex is absent on both sides in a cerebral affection, it indicates a diffuse disease of the brain; its absence on one side indicates a local affection of the opposite half of the brain.

The **cremasteric, conjunctival, mammillary, pupillary,** and **nasal** reflexes may also be specially investigated. In hemiplegia complicated with cerebral lesions, the reflexes on the paralysed side are diminished, whilst not unfrequently the patellar reflex may be increased. In *extensive* cerebral affections accompanied by coma the reflexes are absent on both sides, including of course those of the anus and bladder (*O. Rosenbach*).

[Horsley finds that in the deepest **narcosis** produced by nitrous oxide gas the superficial reflexes (*e.g.*, plantar, conjunctival) are abolished, while the deep (knee-jerk) remain. Anæmia of the lumbar enlargement (compression of the abdominal aorta) causes disappearances of both reflexes (*Prévost*). Chloroform and asphyxia abolish the deep as well as the superficial reflexes. Horsley regards the so-called deep reflex or knee-jerk not as depending on a centre in the cord, but the contraction of the rectus femoris is due to local irritation of the muscle from sudden elongation.]

Deep or so called **Tendon Reflexes.**—Under pathological conditions, special attention is directed to the so-called tendon reflexes [or better still, **tendon reactions**], which depend upon the fact that a blow upon a tendon (*e.g.*, the quadriceps femoris, tendo Achillis, &c.) discharges a contraction of the corresponding muscle (*Westphal, Erb*, 1875). The patellar tendon reflex [also called "**knee phenomenon**"] or simply "knee reflex" or "**knee-jerk,**" is invariably absent in cases of ataxic tabes dorsalis, while in spastic spinal paralysis it is abnormally strong and extensive (*Erb*). [The "**knee-jerk**" is elicited by percussing the ligamentum patellæ, and is due to a *single* spasm of the rectus. The latent period is 0·03 to 0·04 second, and it is argued by Waller and others that it is doubtful if this reaction is subserved by a spinal nervous arc, while admitting the effect of the spinal cord in modifying the response of the muscle.] Section of the motor nerves abolishes the patellar phenomenon in rabbits (*Schultze*), and so does section of the cord opposite the 5th and 6th lumbar vertebræ (*Tschirjew*). Landois finds that in his own person the contraction occurs 0·048 second after the blow upon the ligamentum patellæ. According to Waller, the patellar reflex and the tendo Achillis reflex occur 0·03 to 0·04 second, and according to Eulenburg, 0·032 second after the blow. According to Westphal, these phenomena are not simple reflex processes, but complex conditions intimately dependent upon the muscle tonus, so that when the tonus of the quadriceps femoris is diminished, the phenomenon is abolished. In order that the phenomenon may take place, it is necessary that the outer part of the posterior column of the spinal cord remain intact (*Westphal*). [The knee-jerk can be increased or reinforced by volitional acts directed to other parts of the body, *e.g.*, by exercising voluntary pressure with the hand (*Jendrássik*) extremely prolonged contractions and high tension enfeeble it.] [A "jaw-jerk" is obtained by suddenly depressing the lower jaw (*Gowers, Beevor, and De Watteville*), and the last observer finds that the latent period is 0·02 second, and if this be the case, it is an argument against these so-called "tendon reflexes" being true reflexes, and that they are direct contractions of the muscles due to sudden stimulation by extension.]

[**Method.**—The **knee-jerk** is easily elicited by striking the patellar tendon with the edge of the hand or a percussion-hammer when the leg is semi-flexed, as when the legs are hanging over the edge of a table or when one leg is crossed over the other. It is almost invariably present in health, but it becomes greatly exaggerated in descending degeneration of the lateral columns and lateral sclerosis.]

[**Ankle clonus** is another tendon reflex, and it is never present in health. If the leg be nearly extended, and pressure made upon the sole of the foot so as suddenly to flex the foot at the ankle, a series of (5 to 7 per second) rhythmical contractions of the muscles of the calf takes place. Gowers describes a modification elicited by tapping the muscles of the front of the leg, the "*front-tap contraction.*" Ankle clonus is excessive in sclerosis of the lateral columns and spastic paralysis.]

[In "ankle clonus" excited by sudden passive flexion of the foot, there is a multiple spasm of the gastrocnemius. Here also the latent period is about 0·03 to 0·04 second, and the rhythm 8 to 10 per second. This short latent period has led some observers to doubt the essentially reflex nature of this act.]

When we are about to **sleep** (§ 374), there is first of all a temporary increase of the reflexes; in the first sleep the reflexes are diminished, and the pupils are contracted. In deep sleep the abdominal, cremasteric, and patellar reflexes are absent; while tickling the soles of the feet and the nose only acts when the stimulus is of a certain intensity. In **narcosis**, *e.g.*, chloroform or morphia, the abdominal, then the conjunctival and patellar reflexes disappear; lastly, the pupils contract (*O. Rosenbach*).

Abnormal **increase** of the reflex activity usually indicates an increase of the excitability of the reflex centre, although an abnormal sensibility of the afferent nerve may be the cause. As the harmonious equilibrium of the voluntary movements is largely dependent upon and regulated by the reflexes, it is evident that in affections of the spinal cord there are frequent disturbances of the voluntary movements, *e.g.*, the characteristic disturbance of motion in attempting to walk, and in grasping movements exhibited by persons suffering from ataxic tabes dorsalis [or as it is more generally called, *locomotor ataxia*].

[The **organic reflexes** include a consideration of the acts of micturition, erection, ejaculation, defæcation, and those connected with the motor and secretory digestive processes, respiration, and circulation.]

362. CENTRES IN THE SPINAL CORD.—**Centres** capable of being excited reflexly, and which can bring about the discharge of certain complicated, yet well-co-ordinated motor acts exist in various parts of the spinal cord. They still retain their activity after the spinal cord is separated from the medulla oblongata; further, those centres lying in the lower part of the spinal cord still retain their activity after being separated from the higher centres, but in the normal intact body they are subjected to the control of higher reflex centres in the *medulla oblongata*. Hence, we may speak of them as subordinate spinal centres. The *cerebrum* also, partly by the production of perceptions, and partly as the organ of volition, can excite or suppress the action of certain of these subordinate spinal centres. [For the significance of the term "Centre," see p. 763.]

1. The **cilio-spinal centre** connected with the **dilatation of the pupil** lies in the lower cervical part of the cord, and extends downwards to the region of the 1st to the 3rd dorsal vertebra. It is excited by diminution of light; *both* pupils always react simultaneously, when *one* retina is shaded. Unilateral extirpation of this part of the spinal cord causes contraction of the pupil on the same side. The motor fibres pass out by the anterior roots of the two lower cervical and two upper dorsal nerves into the cervical sympathetic (§ 392). Even the idea of darkness may sometimes, though rarely, cause dilatation of the pupil (*Budge*).

In goats and cats, this centre, even after being separated from the medulla oblongata, can be excited directly by dyspnœic blood, and also reflexly by the stimulation of sensory nerves, *e.g.*, the median, especially when the reflex excitability of the cord is increased by the action of strychnin or atropin (*Luchsinger*). For the dilator centre in the medulla oblongata, see § 367, 8.

2. The **ano-spinal centre**, or centre controlling the act of **defæcation**. The afferent nerves lie in the hæmorrhoidal and inferior mesenteric plexuses, the centre at the 5th (dog) or 6th to 7th (rabbit) lumbar vertebra; the efferent fibres arise from the pudendal plexus and pass to the sphincter muscles. For the relation of this centre to the cerebrum see § 160. After section of the spinal cord [in dogs], Goltz observed that the sphincter contracted rhythmically upon the finger introduced into the anus; the co-ordinated activity of the centre therefore would seem to be possible only when the centre remains in connection with the brain.

3. The **vesico-spinal centre** for regulating micturition, or Budge's vesico-spinal centre. The centre for the *sphincter* muscle lies at the 5th (dog) or the 7th (rabbit) lumbar vertebra, and that for the muscles of the *bladder* somewhat higher. The centre acts only in a properly co-ordinated way in connection with the brain (§ 280).

4. The **erection centre** also lies in the lumbar region (§ 436). The afferent nerves are the sensory nerves of the penis; the efferent nerves for the deep artery of the penis are the **vaso-dilator nerves**, arising from the 1st to 3rd sacral nerves, or Eckhard's **nervi erigentes**—while the motor nerves for the ischio-cavernosus and deep transverse perineal muscles arise from the 3rd to 4th sacral nerves (§ 356). The latter may also be excited voluntarily, the former also partly by the brain, by directing the attention to the sexual activity. Eckhard observed erection to take place after stimulation of the higher regions of the spinal cord, as well as of the pons and crura cerebri.

5. The **ejaculation centre.** The afferent nerve is the dorsal of the penis, the centre (Budge's genito-spinal centre) lies at the 4th lumbar vertebra (rabbit); the motor fibres of the vas deferens arise from the 4th and 5th lumbar nerves, which pass into the sympathetic, and from thence to the vas deferens. The motor fibres for the bulbo-cavernosus muscle, which ejects the semen from the bulb of the urethra, lie in the 3rd and 4th sacral nerves (perineal).

6. The **parturition centre** lies at the 1st and 2nd lumbar vertebræ (§ 453); the afferent fibres come from the uterine plexus, to which also the motor fibres proceed (*Körner*). Goltz and Freusberg observed that a bitch became pregnant after its spinal cord was divided at the 1st lumbar vertebra.

7. **Vaso-motor Centres.**—Both vaso-motor and vaso-dilator centres are distributed throughout the whole spinal axis. To them belongs the centre for the *spleen*, which in the dog is opposite the 1st to 4th cervical vertebræ (*Bulgak*). They can be excited reflexly, but they are also controlled by the dominating centre in the medulla oblongata (§ 371). Psychical disturbance (cerebrum) influences them (§ 377).

[8. Perhaps there are **vaso-dilator centres** (§ 372).]

9. The **sweat centre** is perhaps distributed similarly to the vaso-motor centre (§ 288).

The reflex movements discharged from these centres are orderly co-ordinated reflexes, and may thus be compared to the orderly reflexes of the trunk and extremities.

Muscle Tonus.—Formerly *automatic* functions were ascribed to the spinal cord, one of these being that it caused a moderate active tension of the muscles—a condition that was termed *muscle tone*, or tonus. The existence of tonus in a striped muscle was thought to be proved by the fact that, when such a muscle was divided, its ends retracted. This is due merely to the fact that all the muscles are stretched slightly beyond their normal length (§ 301). Even paralysed muscles, which have lost their muscular tone, show the same phenomenon. Formerly the stronger contraction of certain muscles, after paralysis of their antagonists, and the retraction of the facial muscles to the sound side, after paralysis of the facial nerve, were also regarded as due to tonus. This result is due to the fact that, during the activity of the intact muscle, the other ones have not sufficient power to restore the parts to their normal median position. The following experiment of Auerbach and Heidenhain is against the assumption of a tonic contraction:—If the muscles of the leg of a decapitated frog be stretched, it is found that they do not elongate after section of the sciatic nerve, or after it is paralysed by touching it with ammonia or carbolic acid.

Reflex Tonus.—If, however, a decapitated frog be suspended in an *abnormal* position, we observe, after section of the sciatic nerve, or the posterior nerve-roots on one side, that the leg on that side hangs limp, while the leg on the sound side is slightly retracted. The sensory nerves of the latter are slightly and continually stimulated by the weight of the limb, so that a slight reflex retraction of the leg takes place, which disappears as soon as the sensory nerves of the leg are divided. If we choose to call this slight retraction tonus, then it is a reflex tonus (*Brondgeest*). (See the experiments of *Harless, C. Ludwig, and Cyon*—§ 355.)

363. EXCITABILITY OF THE SPINAL CORD.—Even at the present time observers are by no means agreed whether the spinal cord, like peripheral nerves, is excitable, or whether it is distinguished by the remarkable peculiarity that most of its conducting paths and ganglia do not react to *direct electrical* and *mechanical* stimuli.

It is contended by some observers that if stimuli be cautiously applied either to white or grey matter, there is neither movement nor sensation (*Van Deen* (1841), *Brown Séquard*). Care

must be taken not to stimulate the roots of the spinal nerves, as these respond at once to stimuli, and thus may give rise to movements or sensations. As the spinal cord conduces to the brain impulses communicated to it from the stimulated posterior roots, but does not itself respond to stimuli which produce sensations, Schiff has applied to it the term "æsthesodic." Further, as the cord can conduct both voluntary and reflex motor impulses, without, however, itself being affected by motor impulses applied to it directly, he calls it "**kinesodic.**"

Schiff's views are as follows:—

1. In the **posterior columns** the sensory root-fibres of the posterior root which traverse these columns give rise to painful impressions, but the proper paths of the posterior columns themselves do not do so. The proof that stimulation of the posterior column produces sensory impressions, he finds in the fact that dilatation of the pupil occurred with every stimulation (§ 292). Removal of the posterior column produces anæsthesia (loss of tactile sensation). Algesia [or the sensation of pain] remains intact, although at first there may even be hyperalgesia.

2. The **anterior columns** are non-excitable, as long as the stimuli are applied only to the proper paths of this column, but movements may follow, both in striped and non-striped muscle, either when the anterior nerve-roots are stimulated, or when, by the escape of the current, the posterior columns are affected, whereby reflex movements are produced.

According to Schiff, therefore, all the phenomena of irritation, which occur when an uninjured cord is stimulated (spasms, contracture), are caused either by simultaneous stimulation of the anterior roots, or are reflexes from the posterior columns alone, or simultaneously from the posterior columns and the posterior roots. Diseases affecting only the anterior and lateral columns alone never produce symptoms of irritation, but always of paralysis. In complete anæsthesia and apnœa, every form of stimulus is quite inactive. According to Schiff's view, all centres, both spinal and cerebral, are inexcitable by artificial means.

Direct Excitability.—Many observers, however, oppose these views, and contend that the **spinal cord is excitable to direct stimulation.** Fick observed movements to take place when he stimulated the white columns of the cord of a frog, isolated for a long distance so as to avoid the escape of the stimulating currents. Sirotinin, also, who stimulated the transverse section of the frog's cord from point to point, obtained contraction of the muscles both by mechanical and electrical stimuli. Biedermann comes to the following conclusions:—The transverse section of a motor nerve is most excitable. Weak stimuli (descending opening shocks) excite the cut surface of the transversely divided spinal cord, but do not act when applied further down. Luchsinger asserts that, after dipping the anterior part of a beheaded snake into warm water, the reflex movements of the upper part of the cord are abolished, while the direct excitability remains.

3. **Excitability of the Vaso-motors.**—The **vaso-constrictor** nerves, which proceed from the vaso-motor centre and run downwards in the lateral columns of the cord, are excitable by all stimuli along their whole course; direct stimulation of any transverse section of the cord constricts all the blood-vessels below the point of section (*C. Ludwig and Thiry*). In the same way, the fibres which ascend in the cord, and increase the action of the vaso-motor centre—*pressor fibres*—are also excitable (*C. Ludwig and Dittmar*—§ 364, 10). Stimulation of these fibres, although it affects the vaso-motor centre reflexly, does not cause sensation.

4. **Chemical stimuli**, such as the application of common salt, or wetting the cut surface with blood, appear to excite the spinal cord.

5. The **motor centres** are directly excited by (1) **blood heated** above 40° C., or (2) by asphyxiated blood, or by sudden and complete anæmia of the cord produced by ligature of the aorta (*Sigm. Mayer*); and (3) also by certain **poisons**—picrotoxin, nicotin, and compounds of barium (*Luchsinger*).

Action of Blood and Drugs.—In experiments of this kind, the spinal cord ought to be divided at the 1st lumbar vertebra, at least twenty hours before the experiment is begun. It is well to divide the posterior roots beforehand to avoid reflex movements. If, in a cat thus operated on, *dyspnœa* be produced, or its *blood overheated*, then *spasms, contraction of the vessels,* and *secretion of sweat* occur in the hind limbs, together with evacuation of the contents of the *bladder* and *rectum*, while there are movements of the *uterus* and the *vas deferens*. Some poisons act in a similar manner. In animals with the medulla oblongata divided, rhythmical

respiratory movements may be produced if the spinal cord has been previously rendered very sensitive by strychnin or overheated blood (*P. v. Rokitansky*, *v. Schroff*—§ 368).

The ganglion-cells of the anterior cornu can be excited **mechanically** (*Birge*), and, according to Biedermann, the grey matter also responds to electrical stimuli.

Hyperæsthesia.—After unilateral section of the cord, or even only of the posterior or lateral columns, there is *hyperæsthesia* on the same side below the point of section (*Fodéra*, 1823, and others), so that rabbits shriek on the slightest touch. The phenomenon may last for three weeks, and then give place to normal or sub-normal excitability. On the sound side the sensibility remains permanently diminished. A similar result has been observed in cases of injury in man. An analogous phenomenon, or a tendency to contraction in the muscles below the section (**hyperkinesia**), has been observed by Brown-Séquard after section of the anterior columns.

Sudden and complete anæmia (by occluding the abdominal aorta in the dog) causes at first spasms (20 seconds), then paralysis (1 min.), then loss of response to sensory (2 mins.), and lastly complete loss of sensibility (3 mins.) (*Fredericq*).

The excitability of the cord is intimately dependent on the continuance of the normal circulation, for ligature of the abdominal aorta rapidly paralyses the lower extremities (*Stenson*, 1667), due to anæmia of the cord (*Schiffer*). After a time the anterior roots of the spinal nerves, and the anæmic part of the grey matter of the cord, undergo degeneration.

364. THE CONDUCTING PATHS IN THE SPINAL CORD.—[**Posterior Root.**—(*a*) The inner part, or **internal radicular fasciculus** is supposed to convey the impressions from tendons and those for touch and locality. When the postero-external column is diseased, as in locomotor ataxia, the deep reflexes, especially the patellar tendon jerk, are enfeebled, or it may be abolished, while the implication of the fibres of the internal fasciculus gives rise to severe pain. (*b*) The **outer radicular fibres** enter the grey matter of the posterior horn, and are supposed to convey the impressions for cutaneous reflexes and temperature. (*c*) The **central fibres** pass directly into the grey matter, and are supposed to conduct painful impressions into the grey matter (fig. 543).]

1. **Localised tactile sensations** (temperature, pressure, and the muscular sense impressions) are conducted upwards through the posterior roots of the ganglia of the posterior cornu, and lastly into the posterior column of the same side.

In **man**, the conducting path from the legs runs in Goll's column, while those for the arm run in the ground-bundle (fig. 553) (*Flechsig*). In **rabbits**, the path of localised tactile impressions lies in the lower dorsal region in the lateral columns (*Ludwig and Woroschiloff*, *Ott and Meade-Smith*).

Anæsthesia.—Section of individual parts of the lateral columns abolishes the sensibility for the parts of the skin connected with the part destroyed, while total section produces the same result for the whole of the opposite side of the body below the section. The condition where tactile and muscular sensibility is lost is known as *anæsthesia*.

2. **Localised voluntary movements** in man are conducted on the same side through the anterior and lateral columns (§§ 358 and 365), in the parts known as the **pyramidal tracts**. The impulses then pass into the cells of the anterior cornu, and thence to the corresponding anterior nerve-roots to the muscles. The exact section experiments of Ludwig and Woroschiloff showed that, in the lower dorsal region of the **rabbit**, these paths were confined to the lateral columns. Every motor nerve-fibre is connected with a nerve-cell in the anterior horn of the frog's spinal cord (*Gaule and Birge*). Section of one lateral column abolishes *voluntary* movement in the corresponding individual muscles below the point of section. It is obvious, from the conduction in 1 and 2, that the lateral columns must increase in thickness and number of fibres from below upwards (*Stilling*, *Woroschiloff*) [see fig. 536].

3. **Tactile reflexes** (extensive and co-ordinated).—The fibres enter by the posterior root, and proceed to the posterior cornu. The groups of ganglionic cells, which control the co-ordinated reflexes, are connected together by fibres which run in the anterior tracts, the anterior ground bundle, and (?) the direct cerebellar tracts (p. 779). The fibres for the muscles which are contracted pass from the motor ganglia outwards through the anterior roots.

In **ataxic tabes dorsalis**, or **locomotor ataxia**, there is a degeneration of the posterior columns, characterised by a peculiar motor disturbance. The voluntary movements can be executed with full and normal vigour, but the finer harmonious adjustments are wanting or impaired, both in intensity and extent. These depend in part upon the normal existence of tactile and muscular impressions, whose channels lie in the posterior columns. After degeneration of the latter, there is not only anæsthesia, but also a disturbance in the discharge of tactile reflexes, for which the centripetal arc is interrupted. But a simultaneous lesion of the sensory nerves alone may in a similar manner materially influence the harmony of the movements, owing to the analgesia and the disappearance of the pathic reflexes (§ 355). As the fibres of the posterior root traverse the white posterior columns, we can account for the disturbances of sensation which characterise the degenerations of these parts (*Charcot and Pierret*). But even the posterior roots themselves may undergo degeneration, and this may also give rise to disturbances of sensation (p. 754). The sensory disturbances usually consist in an abnormal increase of the tactile or painful sensations, with lightning pains shooting down the limbs, and this condition may lead to one where the tactile and painful sensations are abolished. At the same time, owing to stimulation of the posterior columns, the tactile sensibility is altered, giving rise to the sensation of formication, or a feeling of constriction [**"girdle sensation"**]. The conduction of sensory impressions is often *slowed* (§ 337). The sensibility of the muscles, joints, and internal parts is altered.

The **maintenance of the equilibrium** is largely guided by the impulses which travel inwards to the co-ordinating centres through the sensory nerves, special and general, deep and superficial. In many cases of locomotor ataxia, if the patient place his feet close together and close his eyes, he sways from side to side, and may fall over, because by cutting off the guiding sensations obtained through the optic nerve, the other enfeebled impulses obtained from the skin and the deeper structures are too feeble to excite proper co-ordination.

4. The **inhibition** of **tactile reflexes** occurs through the anterior columns (?); the impulses pass from the anterior column at the corresponding level into the grey matter, where they form connections with the reflex conducting apparatus.

5. The conduction of **painful** impressions occurs through the posterior roots, and thence through the whole of the grey matter. There is a partial decussation of these impulses in the cord, the conducting fibres passing from one side to the other. The further course of these fibres to the brain is given in § 365.

If all the grey matter be divided, except a small connecting portion, this is sufficient to conduct painful impressions. In this case, however, the conduction is *slower* (*Schiff*). Only when the grey matter is completely divided is the conduction of painful impressions from below completely interrupted. This gives rise to the condition of **analgesia**, in which, when the posterior columns are still intact, tactile impressions are still conducted. This condition is sometimes observed in man during incomplete narcosis from chloroform and morphia (*Thiersch*). Those poisons act sooner on the nerves which administer to painful sensations than on those for tactile impressions, so that the person operated on is conscious of the contact of a knife, but not of the painful sensations caused by the knife dividing the parts. As painful impressions are conducted by the whole of the grey matter, and as the impressions are more powerful the stronger the painful impression, we may thus explain the so-called **irradiation of painful impressions**. During violent pain, the pain seems to extend to wide areas; thus, in violent toothache, proceeding from a particular tooth, the pain may be felt in the whole jaw, or it may be over one side of the head.

According to Bechterew, the paths for the conduction of painful impressions lie in the anterior part of the lateral column (dog, rabbit).

The experiments of Weiss on dogs, by dividing the lateral column at the limit of the dorsal and lumbar regions, showed that each lateral column contains sensory fibres for *both* sides. The chief mass of the motor fibres remains on the *same* side. Section of *both* lateral columns abolishes completely sensibility and motility on both sides. The anterior columns and the grey matter are not sufficient to maintain these.

6. The conduction of **spasmodic, involuntary, inco-ordinated** movements takes place through the grey matter, and from the latter through the anterior roots.

It occurs in epilepsy, poisoning with strychnin, uræmic poisoning, and tetanus (§ 360, II.). The anæmic and dyspnœic spasms are excited in and conducted from the medulla oblongata, and communicated through the whole of the grey matter.

7. The conduction of **extensive reflex spasms** takes place from the posterior roots, and then to the cells of the anterior cornu, above and below the plane of the entering impulse (fig. 458), and, lastly, into the anterior roots, under the conditions already referred to in § 360, II.

8. The **inhibition of pathic reflexes** occurs through the anterior columns downwards, and then into the grey matter to the connecting channels of the reflex organ, into which it introduces resistance.

9. The **vaso-motor** fibres run in the lateral columns (*Dittmar*), and, after they have passed into the ganglia of the grey matter at the corresponding level, they leave the spinal cord by the anterior roots. They reach the muscles of the blood-vessels either through the paths of the spinal nerves, or they pass through the rami communicantes into the sympathetic, and thence into the visceral plexuses (§ 356).

Section of the spinal cord paralyses all the vaso-motor nerves below the point of section; while **stimulation** of the peripheral end of the spinal cord causes contraction of all these vessels. [Ott's experiments on cats show that the vaso-motor fibres run in the lateral columns, and that they as well as the sudorific nerves decussate in the cord.]

10. **Pressor** fibres enter in the posterior roots, run upwards in the lateral columns, and undergo an incomplete decussation (*Ludwig and Miescher*).

They ultimately terminate in the *dominating vaso-motor centre* in the medulla oblongata, which they excite reflexly. Similarly, *depressor* fibres must pass upwards in the spinal cord, but we know nothing as to their course.

11. From the **respiratory centre** in the medulla oblongata, **respiratory nerves** run downwards in the lateral columns on the *same* side, and after forming connections with the ganglia of the grey matter pass through the anterior roots into the motor nerves of the respiratory muscles (*Schiff*).

Unilateral, or total destruction of the spinal cord, the higher up it is done, accordingly paralyses more and more of the respiratory nerves, on the same or on both sides. Section of the cord above the origin of the phrenic nerves causes death in some animals, owing to the paralysis of these nerves of the diaphragm (§ 113).

In **pathological cases**, in degeneration of, or direct injury to, the spinal cord or its individual parts, we must be careful to observe whether there may not be present simultaneously paralytic and irritative phenomena, whereby the symptoms are obscured.

Degeneration of the posterior columns without involving the posterior root-fibres causes loss of tactile sensibility, the feeling for heat remaining intact. Degeneration of the nerve-cells of the anterior cornu, as in infantile spinal paralysis, causes paralysis of the motor nerves proceeding from them, and at the same time the muscles supplied by these nerves rapidly undergo atrophy, as these cells are the trophic centres both for these nerves and the muscles they supply. Degeneration of the posterior cornu causes disturbance of the cutaneous sensibility and produces trophic changes in the skin.

If the abdominal aorta be temporarily closed in rabbits, there results permanent motor and sensory paralysis, and in the region of the cord rendered anæmic the ganglion cells and fibres of the anterior cornu undergo degeneration (*Ehrlich, Singer*).

[**Complete transverse section of the cord** results **immediately** in complete paralysis of motion and sensation in all the parts supplied by nerves below the seat of the injury, although the muscles below the injury retain their normal trophic and electrical conditions. There is a narrow hyperæsthetic area at the upper limit of the paralysed area, and when this occurs in the dorsal region it gives rise to the feeling of a belt tightly drawn round the waist, or the "girdle sensation." There is also vaso-motor paralysis below the lesion, but the blood-vessels soon regain their tone, owing to the subsidiary vaso-motor centres in the cord. Thus the person has no voluntary control over the parts supplied by nerves coming off below the injury. If the section be in the lower dorsal region, the processes of micturition and defæcation cease to be under voluntary control, but after a time these acts

can be executed reflexly. The **remote effects** come on much later, and are secondary descending degeneration in the crossed and direct pyramidal tracts and ascending degeneration in the postero-internal columns (fig. 558). According to the seat of the lesion, the functions of the bladder and rectum may be interfered with. Injury to the upper cervical region sometimes causes hyperpyrexia. Of course section high up in the cervical region will interfere with the respiratory movements, the result depending on the level at which the section is made.]

[**Unilateral section** results in paralysis of voluntary motion in the muscles of the same side supplied by nerves given off below the seat of the injury, although the muscles do not atrophy, but when secondary descending degeneration occurs they become rigid, and exhibit the ordinary signs of contracture. There is vaso-motor paralysis on the same side, although this passes off below the injury, while the ordinary and muscular sensibility are diminished on both sides (fig. 562). There is bilateral anæsthesia. On the opposite side there is total anæsthesia and analgesia below the lesion, but on the same side in the dorsal region there is a narrow circular anæsthetic zone (fig. 562, *b*), corresponding to the sensory nerve-fibres destroyed at the level of the section. The sensory nerves decussate shortly after they enter the cord, hence the anæsthesia on the opposite side, but they do not cross at once, but run obliquely upwards before they enter the grey matter of the opposite side, so that a unilateral section will involve some fibres coming from the same side, and hence the slightly diminished sensibility in a circular area on the same side. There is a narrow hyperæsthetic area on the same side as the lesion, at the upper limit of the paralysed cutaneous area (fig. 562, *c*), due perhaps to stimulation of the cut ends of the sensory fibres on that side. In man there is hyperæsthesia (to touch, tickling, pain, heat, and cold) on the parts below the lesion on the same side, but the cause of this is not known. The **remote** effects are due to the usual descending and ascending degeneration which set in.]

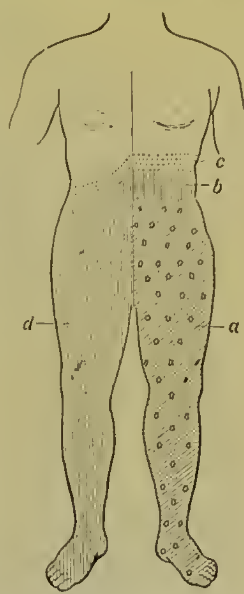


Fig. 562.

Diagrammatic representation of a lesion of the *left* half of the spinal cord in the dorsal region. (*a*) oblique lines, motor and vaso-motor paralysis; (*b*, *d*), complete anæsthesia; (*a*, *c*), hyperæsthesia of the skin.

[In **monkeys**, after hemi-section of the cord in the dorsal region, there is paralysis of voluntary motion and retention of sensibility with vaso-motor paralysis of the same side, and retention of voluntary motion with anæsthesia and analgesia on the opposite side. The existence of hyperæsthesia on the side of the lesion is not certain in these animals, but there is no doubt of it in man. Ferrier also finds (in opposition to Brown-Séquard) that the muscular sense is paralysed, as well as all other forms of sensibility, on the side opposite to the lesion, but unimpaired on the side of the lesion. The muscular sense, in fact, is entirely separable from the motor innervation of muscle (*Ferrier*). The power of emptying the bladder and rectum was not affected.]

The Brain.

365. GENERAL SCHEMA OF THE BRAIN.—In an organ so complicated in its structure as the brain, it is necessary to have a general view of the chief arrangements of its individual parts. Meynert gave a plan of the general arrangement of this organ, and although this plan may not be quite correct, still it is useful in the study of brain function. The average **weight** of the brain is in man about 1358 grams, and in woman 1220 grams (*Bischoff*).

[A special layer of **grey matter** of the cerebrum is placed externally and spread as a thin coating over the white matter or **centrum ovale**—which lies internally, and consists of nerve-fibres or the white matter. That part lying in each hemisphere is the centrum semi-ovale. The grey matter is folded into **gyri** or **convulsions** separated from each other by **fissures** or **sulci**. Some of the latter are very marked, and serve to separate adjacent **lobes**, while the lobes themselves are further subdivided by sulci into convolutions. For a description of the lobes see § 375. Some masses of grey matter are disposed at the base of the brain, forming the **corpus striatum** (projecting into the lateral ventricles), which in reality is composed of two parts, the nucleus caudatus and lenticular nucleus (fig. 563, *b*), the **optic thalamus**, which lies behind the former, and bounds the 3rd ventricle (fig. 563, *d*), the **corpora quadrigemina** lying on the upper surface of the crura cerebri (fig. 563, *hi*); within the tegmentum of the crura cerebri are the **red nucleus** and **locus niger** (fig. 628). Lastly, there is the continuation of the grey matter of the cord up through the medulla, pons, and around the iter, forming the **central grey tube**, and terminating anteriorly at the tuber cinereum. These various parts are connected in a variety of ways with each other, some by transverse fibres stretching between the two sides of the brain, while other longitudinal fibres bring the hinder and lower parts into relation with the fore parts.]

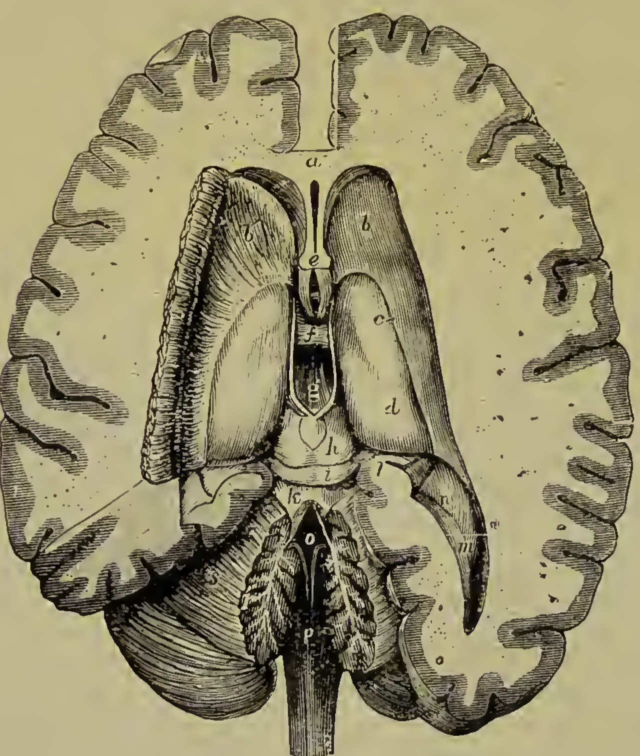


Fig. 563.

Dissection of the brain from above, showing the lateral 3rd and 4th ventricles, with the basal ganglia, and surrounding parts. *a*, knee of the corpus callosum ; *b*, anterior part of the right corpus striatum ; *b'*, grey matter dissected off to show white fibres ; *c*, points to tænia semicircularis ; *d*, optic thalamus ; *e*, anterior pillars of fornix, with 5th ventricle in front of them, between the two laminæ of the septum lucidum ; *f*, middle or soft commissure ; *g*, 3rd ventricle ; *h*, *i*, corpora quadrigemina ; *k*, superior cerebellar peduncle ; *l*, hippocampus major ; *m*, posterior cornu of lateral ventricle ; *n*, eminentia collateralis ; *o*, 4th ventricle ; *p*, medulla oblongata ; *s*, cerebellum, with *r*, arbor vitæ.

[Under cover of the occipital lobes, but connected with the cerebrum in front, and the spinal cord below, is the **cerebellum**, which has its grey matter externally and its white core internally. Thus we have to consider cerebro-spinal and cerebello-spinal connections.]

[**Meynert's Projection Systems.**—The cortex of the cerebrum consists of convolutions and sulci, the "**peripheral grey matter**" (fig. 564, C), which is recognised as a nervous structure, from the presence in it of numerous ganglionic cells (§ 358, 1). From it proceed all the motor fibres which are excited by the will, and to it proceed all the fibres coming from the organs of special sense and sensory organs, which give rise to the psychical perception of external impressions. [In fig. 564 the decussation of the sensory fibres is represented as occurring near the medulla oblongata. It is more probable that a large number of the sensory fibres

decussate shortly after they enter the cord, as is represented in fig. 569. Some of the sensory fibres, however, decussate in the medulla oblongata.]

First Projection System.—The channels lead to and from the cortex cerebri, some of them

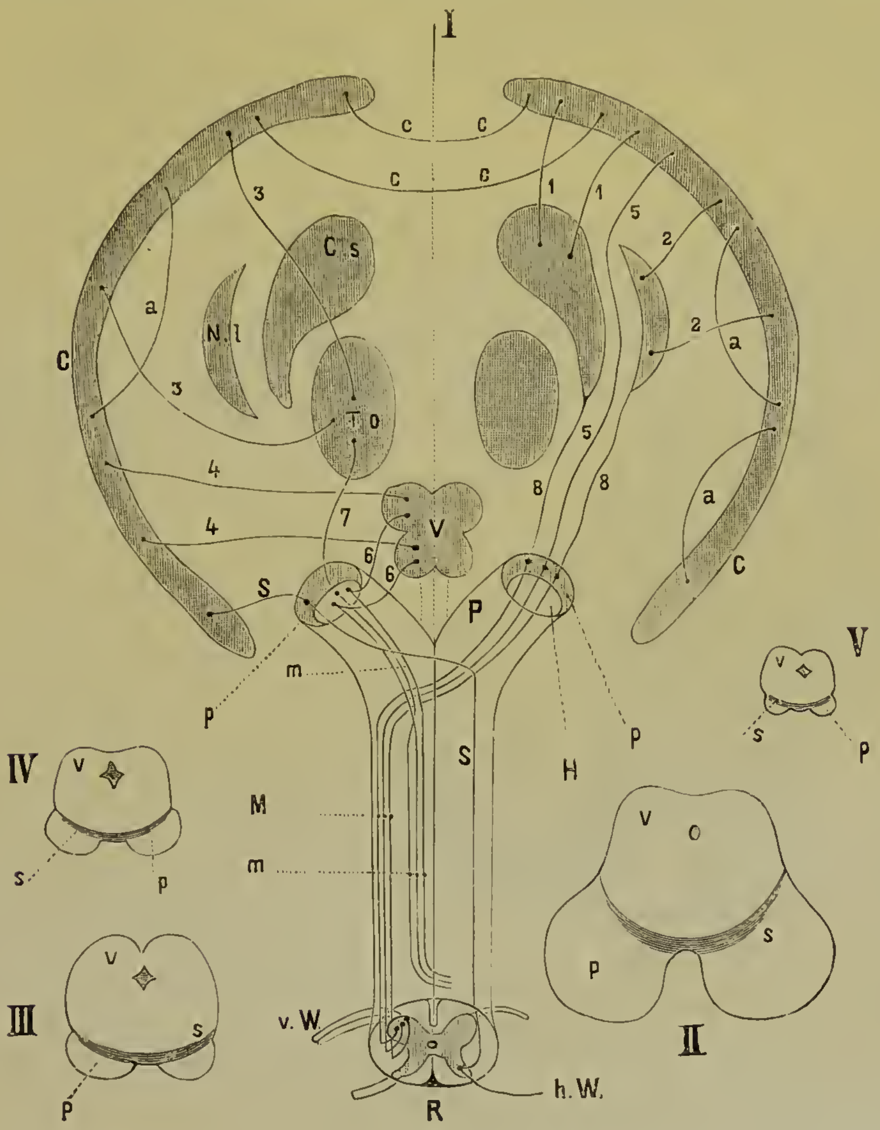


Fig. 564.

I, Scheme of the brain.—C, C, cortex cerebri; C.*s*, corpus striatum; N.*l*, nucleus lenticularis; T.*o*, optic thalamus; *v*, corpora quadrigemina; P, pedunculus cerebri; H, tegmentum; and *p*, crusta; 1, 1, corona radiata of the corpus striatum; 2, 2, of the lenticular nucleus; 3, 3, of the optic thalamus; 4, 4, of the corpora quadrigemina; 5, pyramidal fibres from the cortex cerebri (*Flechsig*); 6, 6, fibres from the corpora quadrigemina to the tegmentum; *m*, further course of these fibres; 8, 8, fibres from the corpus striatum and lenticular nucleus to the crusta of the pedunculus cerebri; M, further course of these; S, S, course of the sensory fibres; R, transverse section of the spinal cord; *v*. W, anterior, and *h*. W, posterior roots; *a*, *a*, association system of fibres; *c*, *c*, commissural fibres. II, Transverse section through the posterior pair of the corpora quadrigemina and the pedunculi cerebri of man—*p*, crusta of the peduncle; *s*, substantia nigra; *v*, corpora quadrigemina, with a section of the aqueduct. III, The same of the dog; IV, of an ape; V, of the guinea-pig. [See p. 798.]

traversing the **basal ganglia**, or ganglia of the cerebrum—the corpus striatum (C.*s*) (composed of the caudate nucleus and lenticular nucleus (N.*l*),) optic thalamus (T.*o*), and corpora quadrigemina—some fibres form connections with cells within this central grey matter. The fibres

which proceed from the cortex through the corona radiata in a radiate direction constitute *Meynert's first projection system*. Besides these, the white substance also contains two other systems of fibres :—(*a*) **Commissural fibres**, such as the corpus callosum and the anterior commissure (*c*, *c*), which are supposed to connect the two hemispheres with each other ; and (*b*) a *connecting* or **association system**, whereby two different areas of the same side are connected together (*a*, *a*). The ganglionic grey matter of the basal ganglia forms the first stage in the course of a large number of the fibres. When they enter the central grey matter, they are *interrupted* in their course. According to Meynert, the corona radiata contains bundles of fibres from the corpus striatum (1, 1), lenticular nucleus (2, 2), optic thalamus (3, 3), and corpora quadrigemina (4, 4).

The second projection system consists of longitudinal bundles of fibres, which proceed downwards and reach the so-called "**central grey tube**," which is the ganglionic grey matter reaching from the 3rd ventricle through the aqueduct of Sylvius, and the medulla oblongata, to the lowest part of the grey matter of the spinal cord. It lines the inner surface of the medullary tube. It is the second stage in the course of the fibres extending from the basal ganglia to the central tubular grey matter. The fibres of this system must obviously vary greatly in length ; some fibres end in the central grey matter above the medulla oblongata, *e.g.*, in the oculo-motor nucleus, while others reach to the level of the last spinal nerves. In the central grey matter, not only is the course of the fibres interrupted, but there is in it an increase in the number of fibres, for far more fibres proceed peripherally from the grey matter of the medulla and spinal cord than are sent to it from the central grey matter of the brain.

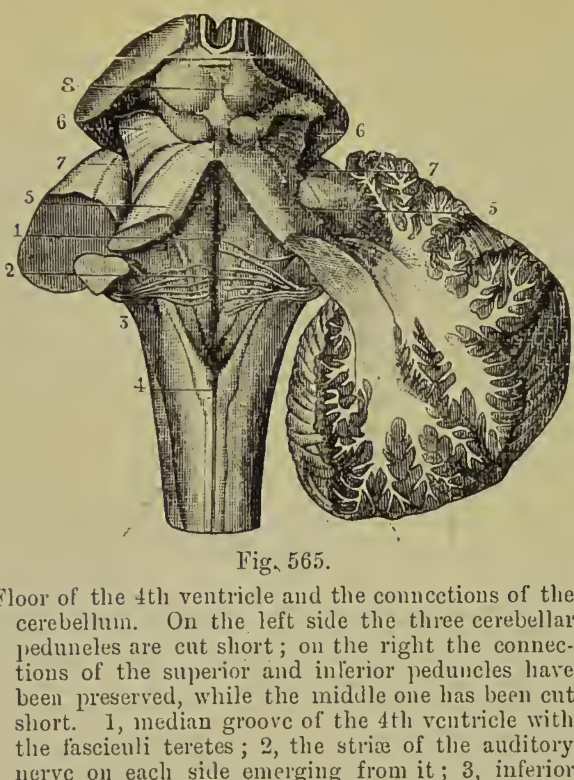


Fig. 565.

Floor of the 4th ventricle and the connections of the cerebellum. On the left side the three cerebellar peduncles are cut short ; on the right the connections of the superior and inferior peduncles have been preserved, while the middle one has been cut short. 1, median groove of the 4th ventricle with the fasciculi teretes ; 2, the striæ of the auditory nerve on each side emerging from it ; 3, inferior peduncle ; 4, posterior pyramid and clava, with the calamus scriptorius above it ; 5, superior peduncle ; 6, fillet to the side of the crura cerebri ; 8, corpora quadrigemina.

As to the arrangement of the fibres in this second system, the fibres descending from the caudate and lenticular nucleus (8, 8) are grouped into a special channel, which descends through the crusta of the cerebral peduncle, and enters the medulla oblongata, or (according to Flechsig) the pons. In the same way there proceeds from the thalamus (S) and corpora quadrigemina (6,6) a bundle which descends through the tegmentum (H) of the cerebral peduncle. Both sets of fibres—those in the crusta and in the tegmentum — come together in the cord.

According to Wernicke, the lenticular nucleus and caudate nucleus are not the parts of the brain into which, from the cerebral cortex and through the corona, radiate fibres enter; but they are independent parts, analogous to the cortex, and from them fibres proceed. These fibres pass into the crusta and run along with those fibres proceeding from the thalamus and corpora quadrigemina.

According to Meynert, the fibres which pass from the thalamus and corpora quadrigemina, through the tegmentum of the cerebral peduncle, are reflex channels ; so that these portions of the brain are centres for certain extensive, co-ordinated reflexes. This is shown by the fact that, after destruction of the voluntary motor paths in animals, the technical completeness of movements, so far as these are discharged reflexly, is still intact. These channels run in the spinal cord, at first on the side (*m*), and probably ultimately cross in the spinal cord itself.

The Third Projection System.—Lastly, from the central tubular grey matter there proceeds the third system, or the **peripheral nerves**, motor and sensory. These are more numerous than the fibres of the second system.

[While there are three concentric tubes in the spinal cord (§ 359), in the part which forms the brain an extra layer of grey matter is added—the **peripheral grey tube**—constituting the cortex of the cerebral hemispheres and cerebellum, and the corpora quadrigemina. Thus, the white matter lies between two concentric masses of grey matter (*Hill*).]

Connections of the Cerebellum.—The cerebellum consists of two somewhat flattened **hemispheres** connected across the middle line by the **middle lobe** or vermiform process which is the fundamental portion of the organ, as it is best developed in lower animals, while as yet the lateral lobes are but small or absent, *e.g.*, in birds. The surface is furrowed by sulci so as to cause it to resemble a series of **folia**, leaflets or **laminæ**; larger fissures divide it into **lobes**. **Peduncles.**—The two **superior peduncles** connect it with the corpora quadrigemina and the crura cerebri. The fibres come from the lower part of the cerebellum and from its dentate nucleus, and a number of these fibres decussate in the upper part of the pons and the tegmentum, some of them becoming connected with the red nucleus in the tegmentum of the opposite side. Some of the fibres seem to connect the cerebellum with the frontal lobes, constituting a fronto-cerebellar tract, and they are also crossed (*Gowers*). When the cerebellum is congenitally absent, these fibres are absent (*Flechsig*). By the two **inferior peduncles** or restiform bodies, it is connected with all the columns of the spinal cord, and it is to be noted that some of the fibres forming these peduncles are connected with the olivary body of the opposite side, so that they decussate. The **middle peduncle** is formed by the transverse fibres of the pons (figs. 517, 566). It is evident that there is a cerebello-spinal as well as a cerebro-spinal connection to be considered.]

[The **grey matter** is external and the white internal, and on section the foliated branched appearance of the cerebellum constitutes the *arbor vitæ*. Within each lateral lobe is a folded mass of grey matter like that in the olivary body, called the **corpus dentatum**, and from its interior white fibres proceed. Stilling describes in the front part of the middle lobe **roof-nuclei**—so called because they lie in the roof of the 4th ventricle. As is shown in fig. 565, the **white fibres** of the superior peduncle pass to the grey matter on the inferior surface of the cerebellum, while the inferior peduncular fibres pass to the superior surface, chiefly of the median part; but both are said to form connections with the corpus dentatum; the middle peduncle is connected with the grey matter of the lateral lobes. The minute structure is described in § 380.]

The distribution of the **blood-vessels** of the brain is of much practical importance. The middle cerebral artery of the Sylvian fissure supplies the motor areas of the brain in animals; in man, the paracentral lobule is supplied by the anterior cerebral artery (*Duret*). The region of the third left frontal convolution, which is the speech-centre, is supplied by a special branch of the middle cerebral. According to Ferrier, that part of the brain, any injury to which causes disturbance of intelligence, is supplied by the anterior cerebral; while those regions, where injury is followed by hemi-anæsthesia, are supplied by the posterior cerebral. It is stated that anæmia of isolated parts of this area of the brain is associated with melancholia in man.

Conduction to and from the cerebrum—Voluntary motor fibres.—The course of the fibres which convey impulses for voluntary motion—the **pyramidal tracts**—proceeds from the **motor regions** of the cerebrum (§§ 375, 378, I.), passing into and through the white matter of the cerebrum through the corona radiata (fig. 566, *a*, *b*, *c*), and converges to the **internal capsule**, which lies between the nucleus caudatus and opticus thalamus internally and the lenticular nucleus externally (fig. 626). They enter the cerebral peduncle, and occupy the middle part of the circumference of the crusta (fig. 566, *Pc*), and pass through the pons on the same side, and from thence into the pyramids (*Py*) of the medulla oblongata. [The motor fibres for the face and tongue occupy the knee of the capsule, those for the arm the anterior third of the posterior segment or limb, and those for the leg the middle third (fig. 566). They pass beneath the optic thalamus, enter the crusta of the cerebral peduncle, and occupy its middle third, or two-fifths, extending almost to the substantia nigra, the fibres for the face being next the

middle line, and those for the leg most external, the fibres for the arm lying between the two. They pass into the pons on the same side, where the fibres for the face (and tongue) cross to the opposite side, to become connected with the nuclei from which the facial and hypoglossal nerves arise (fig. 566 *f*). The fibres for the arm and leg (and trunk) continue their course to the medulla oblongata, where they form the anterior pyramids. In the pons, the pyramidal tracts are broken up into bundles lying between its superficial and deep transverse fibres, and surrounded by grey matter (fig. 629); but they have no connection with the grey matter of the pons. By far the greater proportion of the fibres cross to the opposite side at the decussation of the pyramids to form the **crossed pyramidal tracts**, or lateral pyramidal tracts, of the lateral column of the opposite side (x). The small uncrossed portion (fig. 566, *b*) is continued as the **direct pyramidal tract** (z) on the same side. The latter fibres, perhaps, supply those muscles of the trunk (*e.g.*, respiratory, abdominal, and perineal), which always act together on both sides. According to other observers, however, they cross to the other side of the cord through the anterior white commissure, and descend in the crossed pyramidal tract or pyramidal tract of the lateral column. The fibres of the pyramidal tracts split up into fine fibrils, which come into connection with the fibrils produced by the subdivision of the processes of the multipolar nerve-cells. Thus, the pyramidal fibres come into connection with the multipolar ganglionic cells of the anterior cornu of the grey matter of the spinal cord at successively lower levels, and from each multipolar cell is directed peripherally a single unbranched axis-cylinder process, which ultimately becomes a nerve-fibre (fig. 566, *a*). The pyramidal tracts thus end in, or at least come into connection with, the multipolar nerve-cells of the grey matter of the spinal cord, from which the anterior roots of the spinal nerves arise.

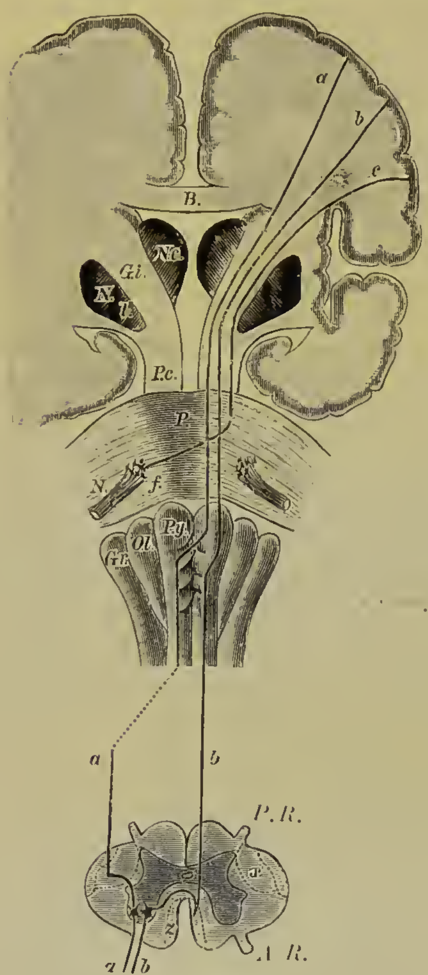


Fig. 566.

Course of the fibres for voluntary movement. *ab*, path for the motor nerves of the trunk; *c*, fibres of the facial nerve; B, corpus callosum; *Nc*, nucleus caudatus; *G.i*, internal capsule; *N.l*, lenticular nucleus; *P*, pons; *N.f*, origin of the facial; *Py*, Pyramids and their decussation; *Ol*, olive, *Gr*, restiform body; PR, posterior root; AR; anterior root; x crossed and z direct pyramidal tracts.

[The course of the pyramidal tracts, and the decussation of these fibres in the medulla oblongata, explain why a hæmorrhage involving the cerebral motor centres, or affecting these fibres in any part of their course above the decussation, results in paralysis of the muscles supplied by the fibres so involved on the *opposite* side of the body. In their passage through the brain, the paths for direct motor impulses are not interrupted anywhere in their course by ganglion-cells, not even in the corpus striatum or pons. They pass in a direct uninterrupted line, until each fibre becomes connected with—or at least its fibrils come into relation with—the processes of a multipolar nerve-cell in the anterior horn of the grey matter of the spinal cord, so that they have the longest course of any fibres in the central nervous system.]

Variation in Decussation.—There are variations as to the number of fibres which cross at the pyramids (*Flechsig*). In some cases the usual arrangement is reversed, and in some rare instances there is no decussation, so that the pyramidal tracts from the brain remain on the same side. In this way we may explain the very rare cases where paralysis of the voluntary movements takes place on the *same* side as the lesion of the cerebrum (*Morgagni, Pierret*). This is **direct paralysis**. [Usually about 90 per cent. of the fibres decussate.]

The **motor cranial nerves** also have centres in the cortex cerebri through which they are excited voluntarily (§ 378). The paths for such voluntary impulses also pass through the internal capsule and the crusta of the cerebral peduncle, but they lie in front of and internal to the pyramidal tracts. [In the internal capsule the fibres for the face (and tongue) lie in the knee, while they occupy the part of the middle of the crusta next the middle line. Their course is then directed across the middle line to their respective nuclei, from which fibres proceed to the muscles supplied by these nuclei.] In fig. 566 *c* shows the course of the fibres to the facial centre. The exact course of many of the fibres is still unknown. The hypoglossal nerve runs with the pyramidal tracts, and behaves like the anterior root of a spinal nerve (§§ 354, 357).

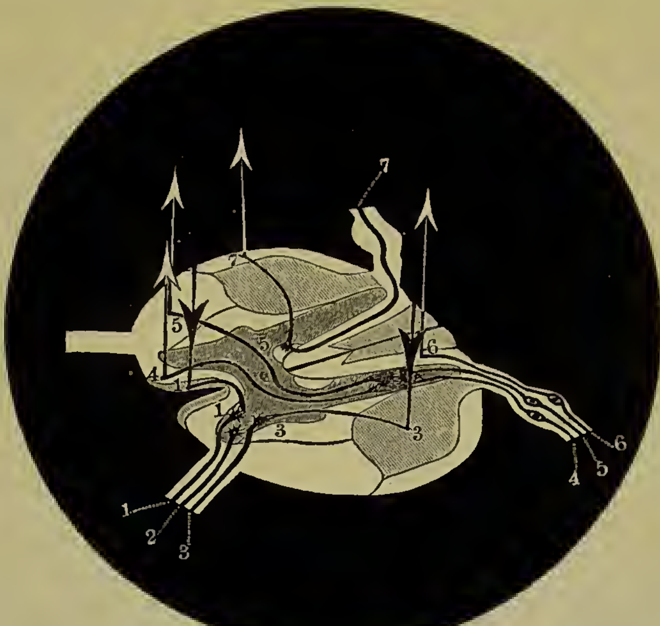


Fig. 567.

Course of the motor and sensory paths in a spinal segment. 1, Anterior pyramidal tract; 3, crossed pyramidal tract; 4 and 5, sensory paths decussating in the cord; 6, sensory paths which do not decussate in the cord; 7, afferent paths leading to Clarke's column and from thence passing as uncrossed fibres upwards *viâ* the direct cerebellar tract; 2, origin of a motor fibre from a ganglionic cell of the anterior cornu.

[**Sensory Paths.** — Our knowledge is by no means precise. Sensory impulses, passing into the cord, enter it by the posterior nerve-roots, and may pass to the cerebrum or cerebellum. There does not seem to be a direct termination of the fibres of the posterior roots in the ganglionic cells of the grey matter of the spinal cord. The fibres always split up first into fibrils. If to the **cerebellum**, the course, probably, is partly to the direct cerebellar tract and posterior column to the restiform body, thence to the cerebellum. It is to be noted, however, that the fibres that proceed to the cerebellum do not do so directly. They enter the cord and run to come into relation with the cells of Clarke's column, so that Clarke's column of cells is their first terminal station, and from the cells of the latter fibres proceed which enter the direct cerebellar tracts (p. 779). If to the **cerebrum**, some of the fibres **cross** the middle line in the cord not far above where they enter and pass to the lateral column, in front of the pyramidal tract. Some enter the posterior column, and others ascend in the grey matter to pass upwards. As the two subdivisions of the posterior column terminate above in the nuclei of the funiculus gracilis and funiculus cuneatus, and this column contains fibres from the posterior root, it is suggested that above the clava and cuneate nucleus the fibres cross in the superior pyramidal decussation to reach the pons and tegmentum. In the medulla, it is probable that those fibres

which do not decussate there do so in the pons, the impulses perhaps travelling upwards in the formatio reticularis, thence into the posterior half of the pons, into the tegmentum of the crus under the corpora quadrigemina, to enter the posterior third of the posterior limb of the internal capsule (fig. 626, S). But, of course, the sensory fibres from the face have to be connected with the sensory centres in the cerebrum, so that the sensory paths from the cord, *i.e.*, from the trunk and limbs, are joined by those from the face in the pons, and they also occupy part of the posterior third of the posterior segment of the internal capsule, so that this important part of the internal capsule conducts sensory impulses from the opposite half of the body. Some of the fibres pass into the optic thalamus, and others enter the white matter of the cerebrum, but their exact course is very uncertain. The sensory fibres derived from the organs of special sense, *e.g.*, the ear, go to the superior temporo-sphenoidal convolution, but whether directly or indirectly we do not know; perhaps some of those for vision traverse the optic thalamus. Some of the afferent fibres perhaps go to the occipital region, and Gowers asserts that some of them go to the parietal and central regions, *i.e.*, to the "motor" regions, for he holds "that disease of the motor cortex often causes impairment of the tactile sensibility."]

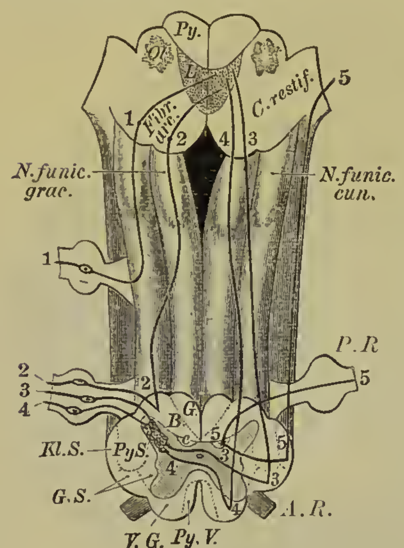


Fig. 568.

Course of the sensory impulses from the posterior roots through the cord to the brain. Compare fig. 569. *A.R.*, anterior, and *P.R.*, posterior roots; *V.G.*, anterior ground bundle; *Py.V.*, direct pyramidal tract; *Py.S.*, crossed pyramidal tract; *G.S.*, lateral tract ground bundle; *Kl.S.*, direct cerebellar tract; G, Goll's column; *B*, postero-external or Burdach's column; Py, pyramids; *Ol*, olivary body; *L*, inter-olivary body or fillet. Arcuate fibres. Restiform body. Funiculus gracilis and funiculus cuneatus of the medulla oblongata.

[Charcot has called the posterior third of the posterior segment of the internal capsule, lying between the posterior part of the lenticular nucleus and the optic thalamus, the "carefour sensitif" or "**sensory crossway**" (fig. 626, S). If it be divided there is hemi-anæsthesia of the opposite side.]

The **posterior columns** appear to **conduct** upwards **sensory impulses** reaching them from the posterior roots. The posterior root after entering the cord shows a division into a median and a lateral bundle. The **median bundle** of each posterior nerve-root as it ascends in the posterior column of its own side tends chiefly to pass outwards near to the posterior cornu (fig. 568, 2). Each successively higher entering root (fig. 568, 1) tends to press inwards the fibres proceeding from the roots below it. Hence in the cervical part of the cord the afferent fibres coming from the lower limbs lie chiefly in Goll's column, while the postero-external column still contains many such fibres from the fore-limbs. The fibres of **Goll's column** end in the nucleus of the **clava**, and those of the **postero-external column** in the **nucleus cuneatus** of the bulb. From these nuclei many fibres proceed to enter the **fillet** or lemniscus (fig. 568, L) of the opposite side (*Edinger*, *Flechsig*). Some of the fibres are said to pass to the cerebellum.

[Of the sensory impulses which pass into the cord some **cross** over to the opposite side; in the cord at higher levels than the plane on which they enter are other fibres. Other impulses, however, are conducted by fibres which remain on the same side of the cord as that on which they enter. They reach the nucleus gracilis and nucleus cuneatus. From these nuclei fibres pass off which pass

forward through the grey matter of the bulb, and decussate with those of the

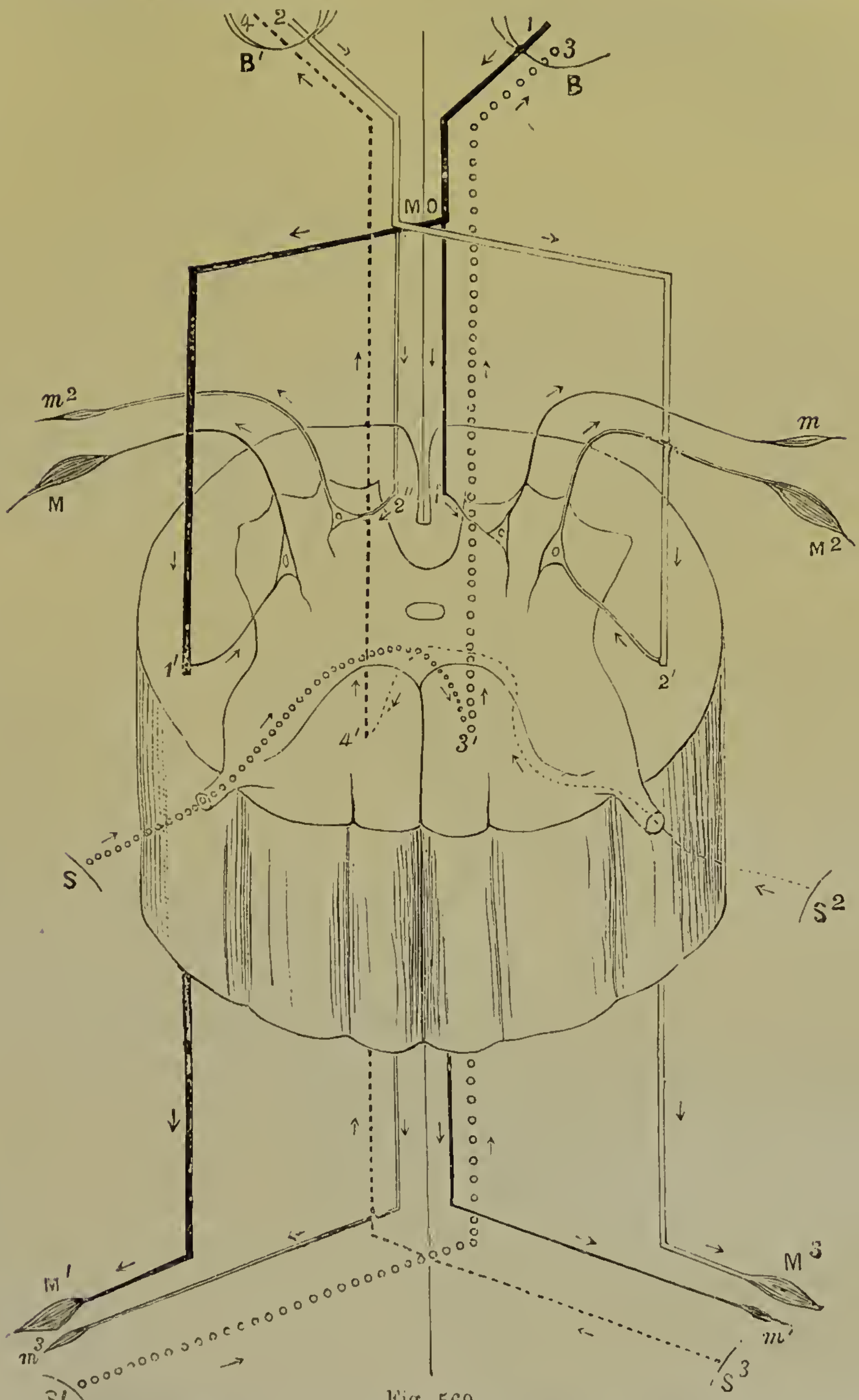


Fig. 569.

Diagram of a spinal segment as a spinal centre and conducting medium. B, right, B′, left cerebral hemisphere ; MO, lower end of medulla oblongata ; 1, motor tract from the right hemisphere, the larger part decussating at MO, and passing down the lateral column of the cord on the opposite side to the muscles M and M′ ; 2, motor tract from the left hemisphere ; S, S′, sensitive areas on the left side of the body ; 3′, 3, the main sensory tract from the left side of the body—it decussates shortly after entering the cord ; S^2, S^3, sensitive areas, and 4′, 4, tracts from the right side of the body. The arrows indicate the direction of the impulses (*Bramwell*). [Here all the sensory fibres are shown as crossing in the cord.]

opposite side. These fibres pass to the fillet or inter-olivary layer, and this constitutes the **supra-pyramidal decussation** of sensory impulses passing to the cerebrum (fig. 571, *d.a.*). This decussation of sensory fibres is best made out in a fœtus of seven months (*Edinger*). Thus some sensory impulses decussate in the cord and others in the bulb.]

The **lateral bundles** of the nerve-roots, composed of coarse and fine fibres (fig. 568, 3, 4), enter the grey matter of the posterior cornu (*Gerlach*, *Lissauer*), and some of them appear to split up into fibres in the grey matter of their own side, while other fibres cross and ascend in the anterior and lateral columns. At the level of the bulb these fibres come to lie, along with their original companions, in the fillet or interolivary body (fig. 568, 4), so that almost all the fibres of the posterior roots lie together, but on the opposite side of the body (*Edinger*). A number of the fibres of the posterior root (fig. 568, 5) appear to end in connection with the cells of Clarke's vesicular column, which is their nutritive or trophic centre. From Clarke's column fibres proceed which pass outwards and upwards in the direct cerebellar tract of the same side. These fibres pass to the restiform body and thence to the cerebellum. These fibres are concerned with the regulation of the equilibrium of the body, and they, together with the cells of Clarke's column, are often diseased in locomotor ataxia.

Sensory Decussation in Cord.—As the greater part of the sensory fibres from the skin **decussate in the spinal cord**, and thus pass to the opposite side of the cord (fig. 569), unilateral section of the spinal cord in man (and monkey—*Ferrier*) abolishes sensibility on the opposite side below the lesion. There is hyperæsthesia of the parts below the seat of the section on the side of the injury (§ 363). From experiments on mammals, Brown-Séquard concludes that the decussating sensory nerve-fibres pass to the opposite side within the cord at different levels, the lowest being the fibres for touch, then those for tickling and pain, and, highest of all, those which administer to sensations of temperature.

All the fibres, therefore, which connect the spinal cord with the grey matter of the brain, undergo a complete decussation in their course. Hence, in man a destructive affection of one hemisphere usually causes complete motor paralysis and loss of sensibility on the *opposite* side of the body. The fibres proceeding from the nuclei of origin of the **cranial nerves** also cross within the cranium.

Not unfrequently the motor paralysis and anæsthesia occur on the *same* side of the head, in which case the lesion (due to pressure or inflammation) involves the cranial nerves lying at the base of the brain.

The **positions of decussation** are (1) in the spinal cord, (2) in the medulla oblongata, and lastly (3) in the pons. The decussation is complete in the peduncle.

Alternate Paralysis.—Gubler observed that unilateral injury to the pons caused paralysis of the facial nerve on the *same* side, but paralysis of the *opposite* half of the body. He concluded that the nerves of the trunk decussate *before* they reach the pons, while the facial fibres decussate within the pons. To these rare cases the name "*alternate hemiplegia*" is given. [When hæmorrhage takes place into the *lower* part of the lateral half of the pons, there may be alternate paralysis, but when the *upper* part of the lateral half is injured, the facial is paralysed on the same side as the body, § 379.]

The olfactory nerve is said not to decussate (?), while the optic nerve undergoes a partial decussation at the chiasma (§ 344). Some observers assert that the fibres of the trochlearis decussate at their origin.

366. THE MEDULLA OBLONGATA OR **BULB.**—[**Structure.**—In the medulla oblongata, the fibres from the cord are rearranged, the grey matter is also much changed, while new grey matter is added. Each half of the medulla oblongata consists of the following parts, from before backwards:—The **anterior pyramid, olivary body, restiform body,** and **posterior pyramid,** or funiculus gracilis (figs. 570, 571, 572). By the divergence of the posterior pyramids and the restiform bodies, the floor of the 4th ventricle is exposed. As the central canal of the cord

gradually comes nearer to the posterior surface of the medulla, it opens into the 4th ventricle. At the lower end of the medulla oblongata, on separating the anterior pyramids, we may see the **decussation of the pyramids**, where the fibres cross over to the lateral columns of the cord. The **anterior pyramid** receives the direct pyramidal tract of the anterior column of the cord from its own side, and the crossed pyramidal tract from the lateral column of the cord of the opposite side (fig. 570). The decussating fibres (crossed pyramidal tract) of the lateral column pass across in bundles to form the decussation of the pyramids. Most of the pyramidal fibres pass through the pons directly to the cerebrum, a few fibres

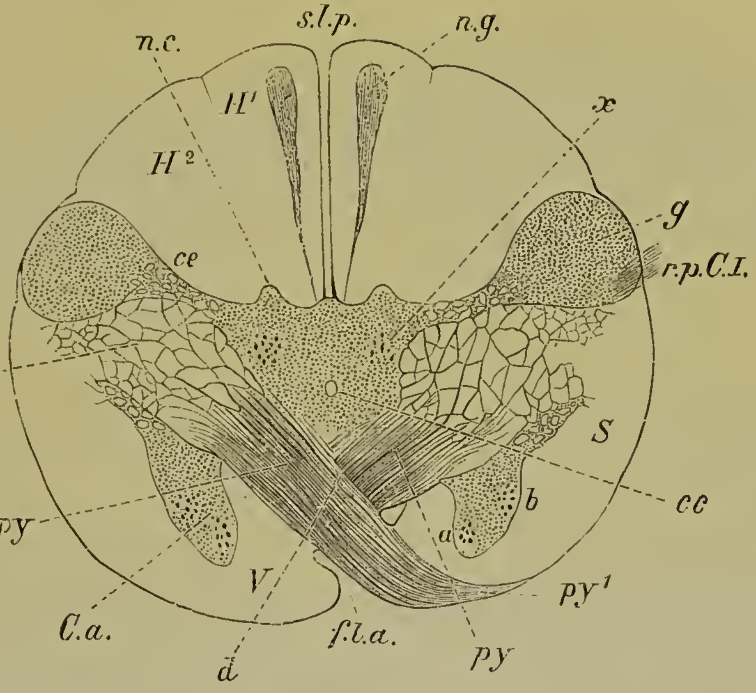


Fig. 570.

Section of the decussation of the pyramids. *fla*, anterior median fissure, displaced laterally by the fibres decussating at *d*; *V*, anterior column; *Ca*, anterior cornu, with its nerve-cells, *a*, *b*; *cc*, central canal; *S*, lateral column; *fr*, formatio reticularis; *ce*, neck, and *g*, head of the posterior cornu; *rpCI*, posterior root of the 1st cervical nerve; *nc*, first indication of the nucleus of the funiculus cuneatus; *ng*, nucleus (clava) of the funiculus gracilis; H^1 funiculus gracilis; H^2, funiculus cuneatus; *slp*, posterior median fissure; *x*, groups of ganglionic cells in the base of the posterior cornu. × 6.

pass to the cerebellum, while some join fibres proceeding from the olivary body to form the olivary fasciculus or fillet.]

[Thus only a part of the anterior column of the cord—direct pyramidal tract—is continued into the anterior pyramid, where it lies external to the fibres which pass to the lateral column of the opposite side. The remainder of the anterior column—the antero-external fibres—are continued upwards, but lie deeper under cover of the anterior-pyramid, where they serve to form part of the formatio reticularis (p. 810).]

[Of the fibres of the *lateral column* of the cord, some, the **direct cerebellar tract**, pass backwards to join the restiform body and go to the cerebellum. These fibres lie as a thin layer on the surface of the restiform body. The *crossed pyramidal* fibres cross obliquely, at the lower end of the medulla, to the anterior pyramid of the opposite side, and in their course they traverse the grey matter of the anterior cornu (fig. 570, *py*). These fibres form the larger and mesial portion of

the anterior pyramid. The remaining fibres of the lateral columns are continued upwards, and pass beneath the olivary body, where they are concealed by this structure and also by the arcuate fibres, but they appear in the floor of the medulla oblongata and are here known as the *fasciculus teres*, which goes to the cerebrum. As they pass upwards, they help to form the lateral part of the formatio reticularis.]

[The **posterior pyramid** of the oblongata is merely the upward continuation of the postero-median column, or funiculus gracilis of the cord. As it passes upwards at the medulla it broadens out, forming the **clava**, which tapers away above. The clava contains a mass of grey matter—the **clavate nucleus.**

[The **restiform body** consists partly of the upward continuation of the postero-external column or funiculus cuneatus of the cord. The funiculus cuneatus contains a mass of grey matter, called the **cuneate** or **triangular nucleus.** Some of the fibres emerging from this nucleus pass to join the restiform body. Above the level of the clava, the funiculus cuneatus forms part of the lateral boundary of the 4th ventricle. Immediately outside this, *i.e.*, between it and the continuation of the posterior nerve-roots, is a longitudinal prominence, which Schwalbe has called the **funiculus of Rolando.** It is formed by the head of the posterior cornu of grey matter coming nearer the surface. It also forms part of the restiform body. Some *arcuate* fibres issue from the anterior median fissure, turn transversely outwards over the anterior pyramids and olivary body, and pass along with the funiculus cuneatus, the funiculus of Rolando, and the direct cerebellar fibres, to enter the corresponding lateral lobe of the cerebellum, all these structures forming its inferior peduncle. Some observers suggest that the funiculus cuneatus and funiculus of Rolando do not pass into the cerebellum.]

[The **olivary body** or **inferior olive** forms a well-marked oval or olive-shaped body, which does not extend the whole length of the medulla (fig. 572, *o*). Above, it is separated from the pons by a groove from which the 6th nerve emerges. In the groove between it and the anterior pyramid arise the strands of the hypoglossal nerve, while in a corresponding groove along its outer surface is the line of exit of the vagus, glosso-pharyngeal, and spinal accessory nerves. It is covered on its surface by longitudinal and arcuate fibres, while in its interior it contains the **dentate** or **olivary nucleus.**]

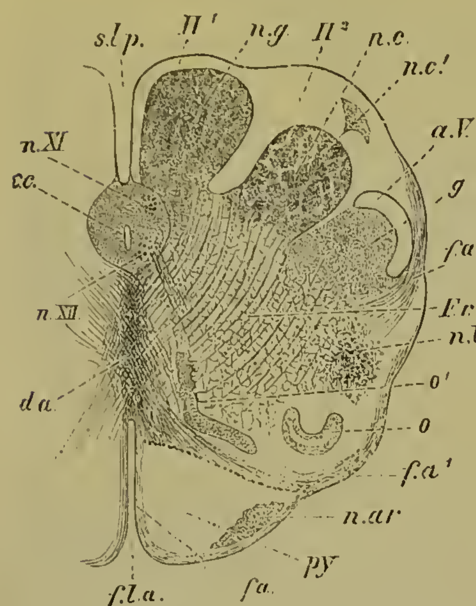
The olivary nucleus is a flask-shaped structure, with folded walls and with a wide open mouth towards the middle line (fig. 571, *o*). It consists of small rounded nerve-cells embedded in a basis of neuroglia and nerve-tissue. Immediately internal and dorsal to it is the **internal parolivary body** or **accessory olivary nucleus** (fig. 572, *oam*,), and external to it is the **external accessory nucleus** (fig. 572, *oal.*). The ninth nerve (fig. 572, XII) runs between the inner accessory nucleus and the olivary body itself.

[The **functions of the olivary bodies** are quite unknown, but it is important to remember that these organs are connected by fibres with the dentate nuclei of the cerebellum. Fibres pass into the olivary body from the posterior column of the cord of the opposite side, and it is also connected with the dentate body of the opposite side, while, as we know, the dentate body is connected with the tegmentum, so that through the left dentate body of the opposite side, the tegmentum of, say, the right crus, is connected with the right olivary body (*Gowers*). In young animals removal of the half of the cerebellum causes atrophy of the olivary nucleus of the opposite side.]

[**Decussation of the pyramids** is the term given to those fibres which cross obliquely in several bundles, at the lower part of the medulla, from the anterior pyramid of the medulla into the lateral column of the cord of the opposite side (fig. 570, *d*) to form its lateral pyramid tracts, or crossed pyramidal tracts. The number of fibres which decussate varies, and in some rare cases all the fibres may cross.]

[The **grey matter** of the medulla is largely a continuation of that of the cord, although it is arranged differently. As the fibres from the lateral column of the cord pass over to form part of the anterior pyramid of the medulla on the opposite side, they traverse the grey matter, and thus cut off the tip of the anterior cornu, which is also pushed backwards by the olivary body, and exists as a distinct mass, the **nucleus lateralis** (fig. 572, *nl*). Part of the anterior grey matter also appears in the floor of the 4th ventricle as the eminence of the fasciculus teres, and

from part of it springs the hypoglossal nerve (fig. 571, *XII*). The neck joining the modified anterior and posterior cornua is much broken up by the passage of longitudinal and transverse fibres through it, so that it forms a **formatio reticularis**, separating the two cornua (fig. 571, *fr*). The caput cornu posterioris comes to be covered higher up by the ascending root of the 5th nerve (fig. 571, *aV*), and arcuate fibres passing to the restiform body. The posterior cornu is also broken up and is thrown outwards, its caput giving rise to part of the elevation seen on the surface and described as the funiculus of Rolando, while part of the base now greatly enlarged forms the grey matter in the funiculus gracilis [clavate nucleus] (fig. 570, *ng*) and funiculus



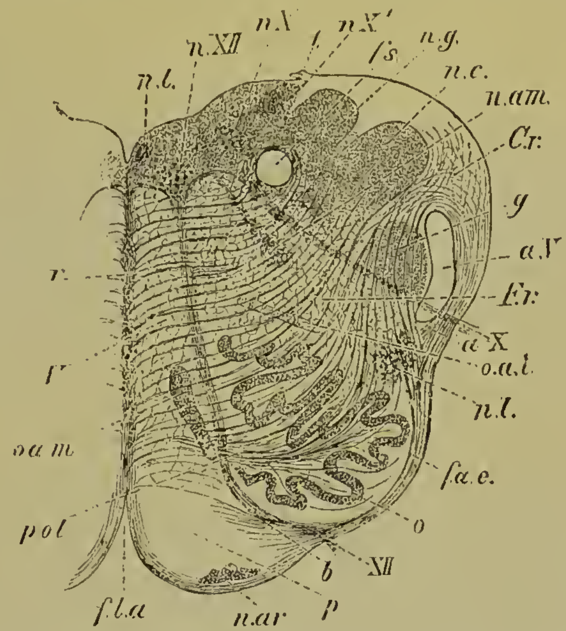


Fig. 571. Fig. 572.

Fig. 571.—Section of the medulla oblongata at the so-called upper decussation of the pyramids. *f.l.a*, anterior, *s.l.p*, posterior median fissure; *n.XI*, nucleus of the accessorius vagi; *n.XII*, nucleus of the hypoglossal; *da*, the so-called superior or anterior decussation of the pyramids; *py*, anterior pyramid; *n.ar*, nucleus arciformis; o^1, median parolivary body; *o*, beginning of the nucleus of the olivary body; *n.l*, nucleus of the lateral column; *F.r*, formatio reticularis; *g*, substantia gelatinosa, with (*a.V*) the ascending root of the trigeminus; *nc*, nucleus of the funiculus cuneatus; $n.c^1$, external nucleus of the funiculus cuneatus; *ng*, nucleus of the funiculus gracilis (or clava); H^1, funiculus gracilis; H^2, funiculus cuneatus; *cc*, central canal; $f.a, f.a^1, f.a^2$, external arciform fibres. × 4. Fig. 572.—Section of the medulla oblongata through the olivary body. *n.XII*, nucleus of the hypoglossal; *nX*, nX^1, more or less cellular parts of the nucleus of the vagus; *XII*, hypoglossal nerve; *X*, vagus; *n.am*, nucleus ambiguus; *n.l*, nucleus lateralis; *o*, olivary nucleus; *oal*, external, and *oam*, internal parolivary body; *f.s*, the round bundle, or funiculus solitarius; *C.r.*, restiform body; *p*, anterior pyramid, surrounded by arciform fibres; *f.a.c*, *p.o.l*, fibres proceeding from the olive to the raphe (pedunculus olivæ); *r* raphe. × 4.

cuneatus [cuneate or triangular nucleus] (fig. 570, *nc*). Nearer the middle line the grey matter of the posterior grey cornu appears in the floor of the 4th ventricle, above the point where the central canal opens into it, as the nuclei of the spinal accessory, vagus, and glosso-pharyngeal nerves.]

[In the floor of the 4th ventricle near the raphe, and quite superficial, is a longitudinal mass of large multipolar nerve-cells, derived from the base of the anterior cornu from which spring the several bundles forming the hypoglossal nerve; it is the **hypoglossal nucleus** (figs. 572, *n.XII*, 573), the nerve-fibres passing obliquely outwards to appear between the anterior pyramid and the olivary body. Internal to it, and next the median groove, is a small mass of cells continuous with those in the raphe, and called the nucleus of the funiculus teres (fig. 572, *n.t*). Around the central canal at the lower part of the medulla is a group of cells (fig. 572, *n.XI*), which becomes displaced laterally as it comes nearer the surface in the floor of the medulla oblongata, where it lies outside the hypoglossal nucleus, and corresponds to the prominence of the ala cinerea (fig. 572, *n.X*); and from it and its continuation upwards arise from below upwards part of the spinal accessory (11th), and the vagus (10th, corresponding to the position of the

eminentia cinerea—fig. 572, X), so that this column of cells forms the **vago-accessorius nucleus.** External to and in front of this is the nucleus for the glosso-pharyngeal nerve. Further up in the medulla, on a level with the auditory striæ and outside the previous column, is a tract of cells from which the auditory nerve (8th) in great part arises; it is the **principal auditory nucleus**, and lies just under the commencement of the inferior cerebellar peduncle (fig. 516, 8′, 8″, 8‴). It consists of an outer and inner nucleus, which extend to the middle line. It forms connections with the cerebellum, and some fibres are said to enter the inferior cerebellar peduncle. This is an important relationship, as we know that the vestibular branch of the auditory nerve comes partly from the semicircular canals, so that in this way these organs may be connected with the cerebellum.]

[**Superadded Grey Matter.**—There is a superadded mass of grey matter not represented in the cord, that of the **olivary body** enclosing a nucleus, the **corpus dentatum**, with its wavy strip of grey matter containing many small multipolar nerve-cells embedded in neuroglia. The grey matter is covered on the surface by longitudinal and transverse fibres. It is open towards the middle line (hilum), and into it run white fibres forming its *peduncle* (fig. 572, *p*, *o*, *l*). These fibres diverge like a fan, some of them ending in connection with the small multipolar cells of the dentate body, while others traverse the lamina of grey matter and pass backwards to appear as arcuate fibres which join the restiform body; others, again, pass directly through to the surface of the olivary body, which they help to cover as the superficial arcuate fibres. The **accessory olivary nuclei** (fig. 571, *o*′, *o*″) are two small masses of grey matter similar to the last, and looking as if they were detached from it, one lying above and external, sometimes called the **parolivary body** and the other slightly below and internal to the olivary nucleus, the latter being separated from the dentate body by the roots of the hypoglossal nerve. The latter is sometimes called the internal parolivary body, or **nucleus of the pyramid.**]

The **formatio reticularis** occupies the greater part of the central and lateral parts of the medulla, and is produced by the intercrossing of bundles of fibres running longitudinally and more or less transversely in the medulla (fig. 571, *fr*). In the more lateral portions are large multipolar nerve-cells, perhaps continued upwards from part of the anterior cornu, while the part next the raphe has no such cells. The longitudinal fibres consist of the upward prolongation of the antero-external columns of the cord, while some seem to arise from the clavate nuclei and olives as arcuate fibres passing upwards. Just above the decussation of the pyramids, some fibres proceed from the clava, and cuneate nuclei, and pass round the central grey matter, and decussate between this and the anterior fissure (p. 806). They form connections between these two nuclei and parts of the brain above, and they form the **superior decussation or sensory decussation.** In the lateral portions the longitudinal fibres are the direct continuation upwards of Flechsig's antero-lateral mixed tracts of the lateral columns (p. 777). The horizontal fibres are formed by **arcuate fibres**, some of which run more or less transversely outwards from the raphe. The *superficial arcuate fibres* (fig. 572, *f*, *a*, *c*) appear in the anterior median fissure, and perhaps come through the raphe from the opposite side of the medulla, curve round the anterior pyramids, form a kind of capsule for the olives, and join the restiform body (p. 808), but they are reinforced by some of the deep arcuate fibres which traverse the olivary body (p. 810). The *deep arcuate fibres* run from the clavate and triangular nuclei horizontally inwards to the raphe, and cross to the other side; others pass from the raphe to the olivary body, and through it to the restiform body in the **raphe**, which contains nerve-cells, some fibres run transversely, others longitudinally, and others from before backwards.]

[**Other Nerve Nuclei—Sixth Nerve.**—Under the elevation called eminentia teres (fig. 516) in front of the auditory striæ, close to the middle line, is a tract of large multipolar nerve-cells. It was once thought to be the common nucleus of the 6th and 7th facial nerves, but Gowers has shown that "the facial ascends to this nucleus, forms a loop round it (some fibres indeed go through it), and then passes downwards, forwards, and outwards, to a column of cells more deeply placed in the medulla than any other nucleus in the lower part." But the 7th has no real origin from this nucleus. **Facial Nerve.**—The nucleus lies deep in the formatio reticularis of the pons under the floor of the 4th ventricle, but outside the position of the nucleus of the 6th (figs. 516, 520, 573). It extends downwards about as far as the auditory striæ, or a little lower. The **fifth nerve** arises from its **motor nucleus** (with large multipolar cells), which lies more superficially above and external to the 6th (fig. 573, 5). The fibres run backwards, where they are joined by fibres from the upper **sensory nucleus**, but another sensory nucleus extends down nearly to the lower end of the medulla (5″). Doubtless this extensive origin brings this nerve into intimate relation with the other cranial nerves, and accounts for the numerous reflex acts which can be discharged through the fifth nerve. Some sensory fibres are said to pass up beneath the corpora quadrigemina (*Gowers*). The **fourth nerve** arises from the valve of Vieussens, *i.e.*, the lamina of white and grey matter which stretches between the superior cerebellar peduncles. It arises, therefore, *behind* the 4th ventricle (fig. 516), but some of the fibres spring from nerve-cells at the lower part of the nucleus of the 3rd nerve. Some fibres also descend in the pons to form a connection with the nucleus of the 6th nerve. The fibres decussate behind the aqueduct, so that in it alone, of all the cranial nerves, decussation occurs

between its nucleus and its superficial origin (*Gowers*). The **third nerve** arises from a tract of cells beneath the aqueduct and near the middle line, and the fibres descend through the tegmentum to appear at the inner side of the crus cerebri. Gowers points out that, in reality, there are three distinct functional centres, (1) for accommodation (ciliary muscle), (2) for the light reflex of the iris, and (3) most of the external muscles of the eyeball. It is important to notice the connection between the nuclei of the 3rd, 4th, and 6th nerves, in relation to the innervation of the ocular muscles.]

[When we trace up the tracts from the cord to the medulla oblongata, two tracts at least pass through the bulb without forming connections with its structures to higher parts, viz., the pyramidal tracts to the cerebrum and the direct cerebellar tract to the cerebellum. Perhaps all the other longitudinal fibres of the cord form connections with some parts of the medulla oblongata, thus the fibres of Goll's column end in the cells of the clava or gracilis nucleus, and those of the postero-external column with the cells of the cuneate nuclei. By means of these nuclei, the fibres of the posterior columns of the cord form indirect connections with the cerebrum and cerebellum. Fibres proceed from both nuclei to form the superior decussation—which after decussation form the inter-olivary layer, which is continued into and forms the chief part of the longitudinal bundle known as the **fillet**, which is continued to the brain. Some fibres proceed from these two nuclei, decussate, and appear as **external arcuate fibres**, which join the restiform body and thus pass to the cerebellum. It has also been suggested that these two nuclei are connected with the cerebellum of the same side.]

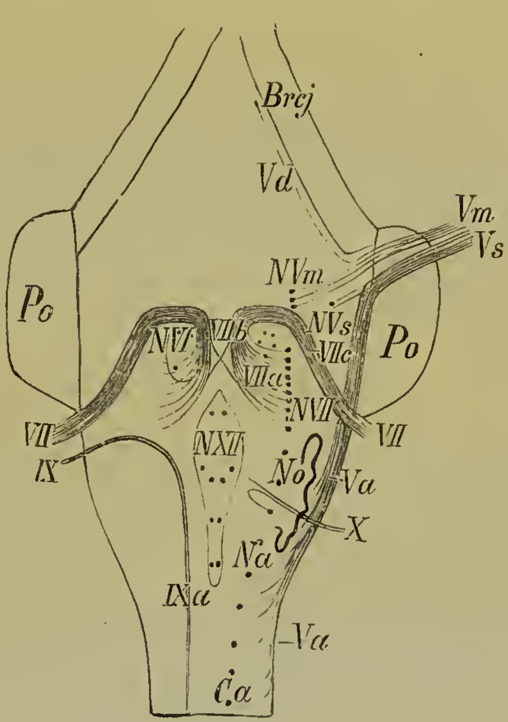


Fig. 573.

Schematic projection of the medulla oblongata. *Po*, pons; *Brcj*, superior cerebellar peduncles; *Va*, ascending; *Vc*, descending; *Vm*, motor; *Vs*, sensory roots of the fifth nerve; *NVm*, motor; *NVs*, sensory trigeminal nucleus; NVII, facial nucleus; VII *a*, *b*, *c*, facial root; VII, point of exit of facial nerve; NVI, nucleus of abducens; IX, *a*, ascending glosso-pharyngeal root; IX, its point of exit; *No*, olivary nucleus; X, vagus (or glosso-pharyngeal nerve), with the origin of certain fine fibres in the nucleus ambiguus; *Na'*, *Ca*, anterior cornu of the spinal cord; *Ca*, *Na*, *NVII*, *NVm*, column of motor nuclei; *NXII*, nucleus of hypoglossal nerve.

Functions of the Bulb. — The medulla oblongata, which connects the spinal cord with the brain, has many points of resemblance with the former. [Like the cord, it is concerned (1) in the **conduction** of impulses.] (2) In it, numerous **reflex centres** are present, *e.g.*, for *simple reflexes* similar to the nerve-centres in the spinal cord, *e.g.*, closure of the eyelids, [so that they subserve the transference of the afferent into efferent impulses]. There are other centres which seem to **dominate** or *control* similar centres placed in the cord, *e.g.*, the great vaso-motor centre, the sweat-secreting, pupil-dilating centres, and the centre for combining the reflex movements of the body. Some of the centres are capable of being excited reflexly (§ 358, 2). (3) It is also said to contain **automatic centres** (§ 358, 3). The normal functions of the centres depend upon the **exchanges of blood-gases**, effected by the circulation of the blood through the medulla. If this gaseous exchange be interrupted or interfered with, as by asphyxia, sudden anæmia, or venous congestion, these centres are first excited, and exhibit a condition of increased excitability, and at last, if they are over-stimulated, they are paralysed. An excessive **temperature** also acts as a stimulus. All the centres however, are not active at the same time, and they do not all exhibit the same

degree of excitability. Normally the respiratory centre and the vaso-motor centre are continually in a state of rhythmical activity. In some animals, the inhibitory centre of the heart remains continually non-excited; in others it is stimulated very slightly under normal conditions simultaneously with the stimulation of the respiratory centre, and only during inspiration. The spasm centre is not stimulated under normal conditions; and during intra-uterine life the respiratory centre remains quiescent. The medulla oblongata, therefore, contains a collocation of nerve-centres which are essential for the maintenance of life, as well as various conducting paths of the utmost importance. We shall treat of the reflex, and afterwards of the automatic centres.

367. **REFLEX CENTRES OF THE MEDULLA OBLONGATA.**—The medulla oblongata contains a number of reflex centres, which minister to the discharge of a large number of co-ordinated movements.

1. **Centre for closure of the eyelids.** The sensory branches of the 5th cranial nerve to the cornea, conjunctiva, and the skin in the region of the eye, are the **afferent** nerves. They conduct impulses to the medulla oblongata, where they are transferred to, and excite part of, the centre of the facial nerve, whence, through branches of the facial, the **efferent** impulses are conveyed to the orbicularis palpebrarum. The centre extends from about the middle of the ala cinerea upwards to the posterior margin of the pons (*Nickell*).

The reflex closure of the eyelids always occurs on *both* sides, but closure may be produced voluntarily on one side (winking). When the stimulation is *strong*, the corrugator and other groups of muscles which raise the cheek and nose towards the eye may also contract, and so form a more perfect protection and closure of the eye. Intense stimulation of the retina causes closure of the eyelids [and in this case the shortest reflex known, the latent period, is 0·05 second (*Waller*)].

2. **Sneezing centre.**—The **afferent** channels are the internal nasal branches of the trigeminus and the olfactory, the latter in the case of intense odours. The **efferent** or motor paths lie in the nerves for the muscles of expiration (§§ 120, 3, and 347, II.). Sneezing cannot be performed voluntarily, [but it may be inhibited by compressing the nasal nerve at its exit on the nose].

3. **Coughing centre.**—According to Kohts, it is placed a little above the inspiratory centre; the **afferent** paths are the sensory branches of the vagus (§ 352, 5, *a*). The **efferent** paths lie in the nerves of expiration and those that close the glottis (§ 120, 1).

4. **Centre for sucking and mastication.**—The **afferent** paths lie in the sensory branches of the nerves of the mouth and lips (2nd and 3rd branches of the trigeminus and glosso-pharyngeal). The **efferent** nerves for *sucking* are (§ 152):—Facial for the lips, hypoglossal for the tongue, the inferior maxillary division of the trigeminus for the muscles which elevate and depress the jaw. For the movements of *mastication*, the same nerves are in action (§ 153); but when food passes within the dental arch, the hypoglossal is concerned in the movements of the tongue, and the facial for the buccinator.

5. **Centre for the secretion of saliva** (p. 250) lies in the floor of the 4th ventricle. Stimulation of the medulla oblongata causes a profuse secretion of saliva when the chorda tympani and glosso-pharyngeal nerves are intact, a much feebler secretion when the nerves are divided, and no secretion at all when the cervical sympathetic is extirpated at the same time (*Grützner*)

6. **Swallowing centre** lies in the floor of the 4th ventricle (§ 156).—The **afferent** paths lie in the sensory branches of the nerves of the mouth, palate, and pharynx (2nd and 3rd branches of the trigeminus, glosso-pharyngeal, and vagus); the **efferent** channels, in the motor branches of the pharyngeal plexus (§ 352, 4). Stimulation of the glosso-pharyngeal nerve does not cause deglutition; on the

contrary, this act is inhibited (p. 271). Hence every act of deglutition excited by stimulation of the palatal nerves or of the superior laryngeal nerve is followed by a feeble abortive contraction of the diaphragm (*Marckwald*).

According to Steiner, every time we swallow there is a slight stimulation of the respiratory centre, resulting in a contraction of the diaphragm. [Kronecker has shown that if a glass of water be sipped slowly, the action of the cardio-inhibitory centre is interfered with reflexly, so that the heart beats much more rapidly, whereby the circulation is accelerated, hence probably the reason why sipping an alcoholic drink intoxicates more rapidly than when it is quickly swallowed (p. 271).]

7. **Vomiting centre** (§ 158).—The relation of certain branches of the vagus to this act are given at § 352, 2, and 12, *d*.

8. **The upper centre for the dilator pupillæ** muscle, the smooth muscles of the orbit, and the eyelids lies in the medulla oblongata. The fibres pass out partly in the trigeminus (§ 347, I., 3), partly in the lateral columns of the spinal cord as far down as the cilio-spinal region, and proceed by the two lowest cervical and the two upper dorsal nerves into the cervical sympathetic (§ 356, A, 1). The centre is normally excited *reflexly* by shading the retina, *i.e.*, by diminishing the amount of light admitted into the eye. It is directly excited by the circulation of dyspnœic blood in the medulla. (The centre for *contracting* the pupil is referred to at §§ 345 and 392.)

The centre may be excited reflexly by stimulation of a sensory nerve, *e.g.*, the sciatic. These afferent fibres pass upwards through both lateral columns to their centre (*Kowalewsky*).

9. There is a subordinate centre in the medulla oblongata, which seems to be concerned in bringing the various reflex centres of the cord into relation with each other. Owsjannikow found that, on dividing the medulla 6 mm. above the calamus scriptorius (rabbit), the *general* reflex movements of the body still occurred, and the anterior and posterior extremities participated in such general movements. If, however, the section was made 1 mm. nearer the calamus, only local partial reflex actions occurred (§ 360, III., 4); [thus, on stimulating the hind-leg, the fore-legs did not react—the *transference* of the reflex was interfered with]. The centre reaches upwards to slightly above the lowest third of the oblongata.

The medulla in the frog also contains the general centre for movements from place to place. Section of this region abolishes the power to move from place to place; when external stimuli are applied, there remains only simple reflex movements (*Steiner*). No reflex movements, such as springing, creeping, or swimming, involving a change of place, result.

Pathological.—The medulla oblongata is sometimes the seat of a typical disease, known as **bulbar paralysis**, or **glosso-pharyngo-labial** paralysis (*Duchenne*, 1860), in which there is a progressive invasion of the different nerve-nuclei (centres) of the cranial nerves which arise within the medulla, these centres being the motor portions of an important reflex apparatus. Usually, the disease begins with paralysis of the *tongue*, accompanied by fibrillar contractions, whereby speech, formation of the food into a bolus, and swallowing are interfered with (§ 354). The secretion of thick, viscid saliva points to the impossibility of secreting a thin watery *facial saliva* (§ 145, A), owing to paralysis of this nerve-nucleus. Swallowing may be impossible, owing to paralysis of the pharynx and palate. This interferes with the formation of *consonants* [especially the linguals, *l*, *t*, *s*, *r*, and, by and by, the labial explosives *b*, *p*] (§ 318, C); the speech becomes nasal, while fluids and solid food often pass into the nose. Then follows paralysis of the branches of the facial to the lips, and there is a characteristic expression of the mouth "as if it were frozen." All the muscles of the face may be paralysed; sometimes the *laryngeal muscles* are paralysed, leading to loss of voice and the entrance of food into the windpipe. The *heart-beats* are often retarded, pointing to stimulation of the cardio-inhibitory fibres (arising from the accessorius). Attacks of *dyspnœa*, like those following paralysis of the recurrent nerves (§ 313, II., 1, and § 352, 5, *b*), and death may occur. Paralysis of the muscles of mastication, contraction of the pupil, and paralysis of the abducens are rare. [This disease is always bilateral, and it is important to note that it affects the nuclei of those muscles that guard the orifices of the mouth, including the tongue, the posterior nares, including the soft palate, and the rima glottidis with the vocal cords.]

368. RESPIRATORY MOVEMENTS AND CENTRE.—**Innervation of the Respiratory Organs.**—[A respiratory act requires the nicely co-ordinated action of many voluntary muscles under the influence of a nerve-centre. Normally the act of respiration is involuntary, although the muscles which execute the act are voluntary, and may be influenced by a direct act of the will. Respiration goes on even when we are asleep and unconscious, and it may still be carried on if all the parts of the brain above a certain part of the medulla oblongata be removed. The co-ordinated impulses proceed from the respiratory centre in the medulla oblongata *viâ* the nerves which supply the muscles of respiration and the movements which are associated with the thoracic respiratory movements, *e.g.*, those of the face, nose, and larynx.]

[Section of the cord below the level of the fifth cervical nerve, *i.e.*, below the origin of the roots of the phrenic nerves, causes arrest of the costal respiration, although the movements of the diaphragm continue. Section of the cord just below the medulla oblongata or bulb causes arrest not only of the costal movements, but also of those of the diaphragm, because the section is above the level of origin of the roots of the phrenic nerves. The respiratory movements, however, in the face—the muscles supplied by the seventh nerve—and those of the larynx (supplied by the vagus) still continue. Section of one phrenic nerve paralyses the diaphragm on that side, and section of both phrenics paralyses both sides of the diaphragm.]

The **respiratory centre** lies in the **medulla oblongata** or **bulb** (*Legallois*, 1811), behind the superficial origin of the vagi, on both sides of the posterior aspect of the apex of the calamus scriptorius, between the nuclei of the vagus and accessorius, and was named by Flourens the vital point, or **nœud vital.** The centre is double, one for each side, and it may be separated by means of a longitudinal incision (*Longet*, 1847), whereby the respiratory movements continue symmetrically on both sides. **Section of vagi.**—If **one vagus** be divided, respiration on the same side is *slowed.* If *both* vagi be divided, the respirations become much *slower* and *deeper*, but the respiratory movements are symmetrical on both sides (fig. 575). [The fact that section of the vagi modifies the respiratory movements shows that impulses must be continually passing upwards in the vagi—from the lungs—to modify the activity of the respiratory centre, and that these impulses influenced the rate and depth of the respiratory discharges]. Stimulation of the *central* end of one vagus, both being divided, causes an arrest of the respiration only on the same side, the other side continues to breathe. The same result is obtained by stimulation of the trigeminus on one side (*Langendorff*). When the centre is divided transversely on one side, the respiratory movements on the *same* side cease (*Schiff*). Most probably the **dominating** respiratory centre lies in the medulla oblongata, and upon it depend the rhythm and symmetry of the respiratory movements; but, in addition, other and **subordinate** centres are placed in the spinal cord, and these are governed by the oblongata centre. If the spinal cord be divided in newly-born animals (dog, cat) below the medulla oblongata, respiratory movements of the thorax are sometimes observed (*Brachet*, 1835).

[If the cord be divided below the medulla, or the cranial arteries ligatured (rabbit), there may still be respiratory movements, which become more distinct if **strychnin** be previously administered, so that Langendorff assumes the existence of a **spinal respiratory centre**, which he finds is also influenced by reflex stimulation of sensory nerves.]

Nitschmann, by means of a vertical incision into the cervical cord, divided the spinal centre into two equal halves, each of which acted on both sides of the diaphragm after the medulla was divided just below the calamus scriptorius. The spinal centres must, therefore, be connected with each other in the cord. The spinal respiratory centre can be excited or inhibited reflexly (*Wertheimer*).

Anatomical.—Schiff locates the respiratory centre near the lateral margins of the grey matter in the floor of the 4th ventricle, but not reaching so far backwards as the ala cinerea. According to Gierke, Heidenhain, and Langendorff, those parts of the medulla oblongata whose

destruction causes cessation of the respiratory movements are single or double strands of nervous matter, containing grey nervous substance with small ganglion cells, and running downwards in the substance of the medulla oblongata. These strands are said to arise partly from the roots of the vagus, trigeminus, spinal accessory, and glosso-pharyngeal (*Meynert*), forming connections by means of fibres with the other side, and descending as far downwards as the cervical enlargement of the spinal cord (*Goll*). According to this view, this strand represents an *inter-central* band connecting the spinal cord (the place of origin of the motor respiratory nerves) with the nuclei of the above-named cranial nerves.

Cerebral Inspiratory Centre.—According to Christiani, there is a *cerebral inspiratory centre* in the optic thalamus in the floor of the 3rd ventricle, which is stimulated through the optic and auditory nerves of the cerebrum and corpora striata having been previously removed; when it is stimulated directly, it deepens and accelerates the *inspiratory* movements, and may even cause a standstill of the respiration in the inspiratory phase. This inspiratory centre may be extirpated. After this operation, an *expiratory* centre is active in the substance of the anterior pair of the corpora quadrigemina, not far from the aqueduct of Sylvius. Martin and Booker describe a second cerebral *inspiratory* centre in the posterior pair of the corpora quadrigemina. These three centres are connected with the centres in the medulla oblongata.

According to Markwald, not only the posterior corpora quadrigemina, but also the sensory nucleus of the trigeminus, is concerned in maintaining the regular respiratory rhythm. In the brain also there are said to exist subordinate **"cerebral respiratory centres."** Ott found on stimulating the tissue between the corpus striatum and optic thalamus that the number of respirations was greatly increased. If this "centre" be destroyed, a dyspnœic respiratory acceleration caused by heat (heat dyspnœa) ceases.

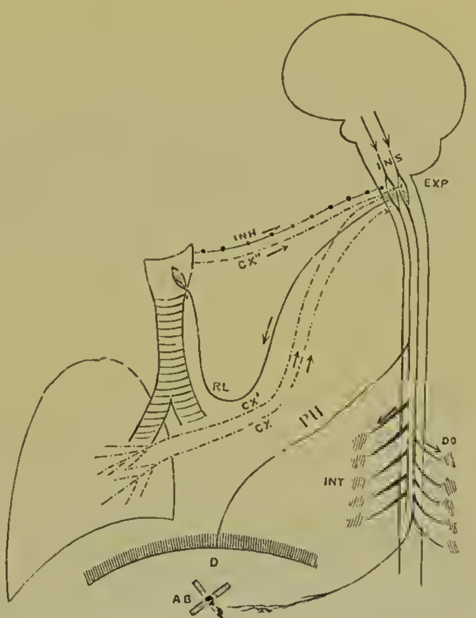


Fig. 574.

Scheme of the chief respiratory nerves. INS, inspiratory, and EXP, expiratory centre—motor nerves are in smooth lines. Expiratory motor nerves to abdominal muscles, AB; to muscles of back, DO. Inspiratory motor nerves. PH, phrenic to diaphragm, D; INT, intercostal nerves; RL, recurrent laryngeal; CX, pulmonary fibres of vagus that excite inspiratory centre; CX′, pulmonary fibres that excite expiratory centre; CX″, fibres of sup. laryngeal that excite expiratory centre; INH, fibres of sup. laryngeal that inhibit the inspiratory centre.

The **respiratory** centre consists of **two centres**, which are in a state of activity alternately—an **inspiratory** and an **expiratory centre** (fig. 574), each one forming the motor central point for the acts of inspiration and expiration (§ 112). The centre is **automatic**, for, after section of all the sensory nerves which can act reflexly upon the centre, it still retains its activity. The degree of excitability and the stimulation of the centre depend upon the **state of the blood**, and chiefly upon the amount of the blood-gases, the O and CO_2 (*J. Rosenthal*). According to the condition of the centre, there are several well-recognised respiratory conditions:—

1. **Apnœa.**—Complete cessation of the respiration constitutes *apnœa*, *i.e.*, cessation of the respiratory movements, owing to the absence of the proper stimulus, due to the blood being saturated with O and poor in CO_2. Such blood saturated with O fails to stimulate the centre, and hence the respiratory muscles are quiescent. This seems to be the condition in the fœtus during intrauterine life. If air be vigorously and rapidly forced into the lungs of an animal by artificial respiration,

the animal will cease to breathe for a time, after cessation of the artificial respiration (*Hook*, 1667), the blood being so arterialised that it no longer stimulates the respiratory centre. If a person takes a series of rapid, deep respirations his blood becomes surcharged with oxygen, and long "**apnœic pauses**" occur.

Apnœic Blood.—A. Ewald found that the arterial blood of apnœic animals was completely saturated with O, while the CO_2 was diminished; the venous blood contained less O than normal—this latter condition being due to the apnœic blood causing a considerable fall of the blood-pressure and consequent slowing of the blood-stream, so that the O can be more completely taken from the blood in the capillaries (*Pflüger*). The amount of O used in apnœa on the whole is not increased (§ 127). Gad remarks that during forced *artificial respiration*, the pulmonary alveoli contain very large amount of atmospheric air; hence, they are able to arterialise the blood for a longer time, thus diminishing the necessity for respiration. According to Gad and Knoll, the excitability of the respiratory centre is reduced during apnœa, and this is caused reflexly during artificial respiration by the distention of the lungs stimulating the branches of the vagus. In quite young animals apnœa cannot be produced (*Runge*).

[**Drugs.**—If the excitability of the respiratory centre be diminished by chloral, apnœa is readily induced, while, if the centre be excited, as by apomorphine, it is difficult to produce it.]

[The state of rest of the respiratory movements, called **apnœa**, and brought about by rapidly increased respirations, was formerly thought to be due to increased oxygenation of the blood. There is, however, room for doubt as to this being the true explanation. In spite of the statement of Ewald, other observers are not agreed that the blood actually does become hyperoxygenated. Moreover, it is very difficult to cause apnœa after section of both vagi. Now section of the vagi can have no effect on the aeration of the blood during rapid artificial respiration, but under these circumstances the afferent impressions from the lungs to the respiratory centre are cut off. The more recent theory suggests that apnœa is due to the rapid respirations exciting the terminations of the inhibitory respiratory fibres in the lungs, and thus presenting a respiratory discharge from the respiratory centre in the medulla oblongata. It has been found that artificial respiration of pure hydrogen in intact animals will cause apnœa. This seems to support the view that ordinary apnœa is in some way intimately related in its cause to the inhibitory impulses generated by rapid inflation of the lungs.]

[**Deglutition Apnœa.**—Kronecker has shown that if a person slowly swallows a glass of water, that the mere act of swallowing arrests the activity of the respiratory centre, and brings about a condition of apnœa, and this even when the nostrils are closed, and no air is admitted to the lungs. This is an additional proof that the production of apnœa has more to do with the generation of inhibitory impulses than with hyperoxygenation of the blood.]

2. **Eupnœa.**—The normal stimulation of the respiratory centre, *eupnœa*, is caused by the blood, in which the amount of O and CO_2 does not exceed the normal limits (§§ 35 and 36).

3. **Dyspnœa.**—All conditions which diminish the O and increase the CO_2 in the blood circulating through the medulla and respiratory centre cause acceleration and deepening of the respirations, which may ultimately pass into vigorous and laboured activity of all the respiratory muscles, constituting *dyspnœa*, when the difficulty of breathing is very great (§ 134). [Changes in the rhythm, § 111.]

During normal respiration, and with the commencement of the need for more air, according to Gad, the gases of the blood excite only the inspiratory centre; while the expiration follows owing to reflex stimulation of the pulmonary vagus by the distention of the lungs (p. 823). He is also of opinion that the normal respiratory movements are excited by the CO_2.

[**Muscular work**, as is well known, increases the respirations and may even cause dyspnœa. This is not due to the nervous connections of the muscles or other organs with the respiratory centre, but to changes in the blood. Geppert and Zuntz have shown, however, that the result cannot be explained by changes in the blood caused either by diminution of O or increase of CO_2. It seems to be due to the blood taking up some as yet unknown products from the contracting muscle, and carrying them to the respiratory centre, which is directly excited by them.

The nature of these substances is unknown. It has been shown that the alkalinity of the blood is reduced by the formation of an acid. The substances, whatever they may be, are not excreted by the urine, and are, therefore, perhaps readily oxidised (*Loewy*). C. Lehmann has proved that, in rabbits, the acidification of the blood produced by muscular exertion plays an important part in the stimulation of the respiratory centre.]

4. **Asphyxia.**—If blood, abnormal as regards the amount and quality of its gases, continue to circulate in the medulla, or if the condition of the blood become still more abnormal, the respiratory centre is *over-stimulated*, and ultimately *exhausted*. The respirations are diminished both in number and depth, and they become feeble and gasping in character; ultimately the movements of the respiratory muscles cease, and the heart itself soon ceases to beat. This constitutes the condition of *asphyxia*, and if it be continued, death from **suffocation** takes place. (Langendorff asserts that in asphyxiated frogs the muscles and grey nervous substance have an acid reaction.) If the conditions causing the abnormal condition of the blood be removed, the asphyxia may be prevented under favourable circumstances, especially by using **artificial respiration** (§ 134); the respiratory muscles begin to act and the heart begins to beat, so that the normal eupnœic stage is reached through the condition of dyspnœa. If the venous condition of the blood be produced slowly and very gradually, asphyxia may occur without there being any symptoms of dyspnœa, as happens when death takes place quietly and very gradually (§ 324, 5).

[**Experiment with crossed heads.**—That the condition of the blood influences the respiratory centre in the medulla oblongata is demonstrated by the following ingenious experiment of Fredericq. Two large rabbits, A and B, are taken, and in both the vertebral arteries are ligatured and the carotids exposed. Cannulæ are introduced into the carotids, so that the blood of the one animal flows into the head of the other. The carotids of the rabbit A carry their blood into the head of rabbit B, and the head of B similarly receives only the blood coming from the body of A. If, at a given moment, A respires air, poor in oxygen, or if its trachea be closed, it is the rabbit B—the one which receives the asphyxiated blood of A—which shows signs of dyspnœa or asphyxical convulsions, whilst A remains quiescent and undisturbed. There is, therefore, an intimate relation between the composition of the blood circulating in the head and the activity of the respiratory movements.]

Amongst the **causes of Dyspnœa** are—(1) **Direct limitation of the activity of the respiratory organs**; diminution of the respiratory surface by inflammation, acute œdema (§ 47), or collapse of the alveoli, occlusion of the capillaries of the alveoli, compression of the lungs, entrance of air into the pleura, obstruction or compression of the windpipe. (2) **Obstruction to the entrance of the normal amount of air** by strangulation, or enclosure in an insufficient space. (3) **Enfeeblement of the circulation**, so that the medulla oblongata does not receive a sufficient amount of blood; in degeneration of the heart, valvular cardiac disease; and artificially by ligature of the carotid and vertebral arteries (*Kussmaul and Tenner*), or by preventing the free efflux of venous blood from the skull, or by the injection of a large quantity of air or indifferent particles into the right heart. (4) **Direct loss of blood**, which acts by arresting the exchange of gases in the medulla (*J. Rosenthal*). This is the cause of the "biting or snapping at the air" manifested by the decapitated heads of young animals, *e.g.*, kittens. [The phenomenon is well marked in the head of a tortoise separated from the body (*W. Stirling*).]

If we study the rapidly fatal effects of these factors on the respiratory activity, we observe that at first the respirations become quicker and deeper, then after an attack of general convulsions, ending in expiratory spasm, there follows a stage of complete cessation of respiration. Before death takes place, there are usually a few "snapping" or gasping efforts at inspiration (*Hogyes, Sigm. Mayer*—§ 111).

Condition of the Blood-Gases.—As a general rule, in the production of dyspnœa, the want of O and the excess of CO_2 act simultaneously (*Pflüger and Dohmen*), but each of these alone may act as an efficient cause. According to Bernstein, blood containing a small amount of O acts chiefly upon the inspiratory centre, and blood rich in CO_2 on the expiratory centre. (1) **Dyspnœa from want of O** occurs during respiration in a space of *moderate* size (§ 133), in spaces where the tension of the air is diminished, and by breathing indifferent gases or those containing no free O. When the blood is freely ventilated with N or H, the amount of CO_2 in the blood may even be diminished, and death occurs with all the signs of asphyxia (*Pflüger*). (2) **Dyspnœa from the blood being overcharged with CO_2** occurs by breathing air containing much CO_2 (§ 133). Air containing much CO_2 may cause dyspnœa, even when the amount of O in the blood is greater than that in the atmosphere (*Thiry*). The blood may even contain more O than normal (*Pflüger*).

Heat Dyspnœa.—An **increased temperature** increases the activity of the respiratory centre (§ 214, II., 3). This occurs when blood warmer than natural flows through the brain, as Fick and Goldstein observed when they placed the exposed carotids in warm tubes, so as to heat the blood passing through them. In this case the heated blood acts directly upon the brain, the medulla and the cerebral respiratory centres (*Gad*). Direct cooling diminishes the excitability (*Fredericq*). When the temperature is increased, vigorous artificial respiration does not produce apnœa, although the blood is highly arterialised (*Ackermann*). Emetics act in a similar manner (*Hermann and Grimm*).

Electrical stimulation of the medulla oblongata, after it is separated from the brain, discharges respiratory movements or increases those already present (*Kronecker and Marckwald*). Langendorff found that electrical, mechanical, or chemical (salts) stimulation usually caused an expiratory effect, while stimulation of the cervical spinal cord (subordinate centre) gave an inspiratory effect. According to Laborde, a superficial lesion in the region of the calamus scriptorius causes standstill of the respiration for a few minutes. If the peripheral end of the vagus be stimulated, so as to arrest the action of the heart, the respirations also cease after a few seconds. Arrest of the heart's action causes a temporary anæmia of the medulla, in consequence of which its excitability is lowered, so that the respirations cease for a time (*Langendorff*).

Conditions affecting the Respiratory Centre.—This centre, besides being capable of being stimulated **directly,** may be influenced by the **will,** and also **reflexly** by stimulation of a number of afferent nerves.

1. By a **voluntary impulse** we may arrest the respiration for a short time, but only until the blood becomes so venous as to excite the centre to increased action.

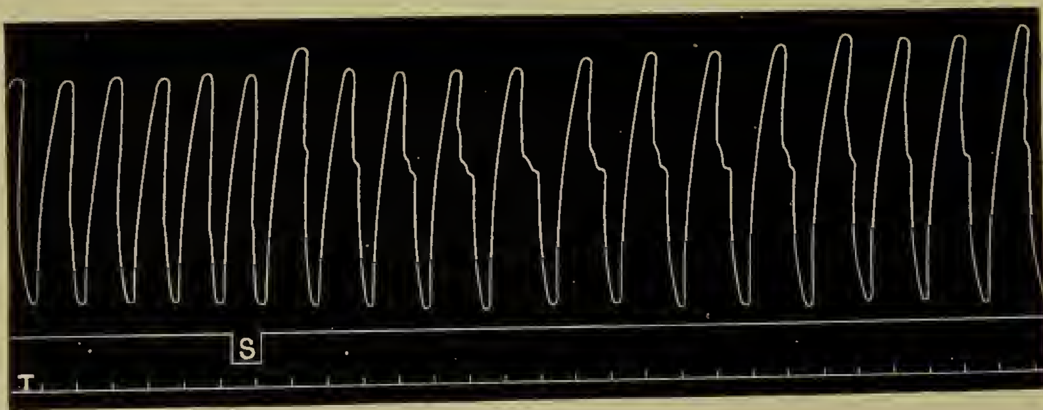


Fig. 575.

Effect on the respiratory movements of section of the second vagus in the rabbit. At S the respirations become slower and deeper. T indicates seconds (*Stirling*).

The number and depth of the respirations may be voluntarily increased for a long time, and we may also voluntarily change the rhythm of respiration.

2. The respiratory centre may be influenced **reflexly** both by fibres which excite it to *increased action* and by others which *inhibit* its action. (*a*) The **exciting** fibres lie in the pulmonary branches of the vagus, in the optic, auditory, and cutaneous nerves; normally their action overcomes the action of the inhibitory fibres. Thus, a cold bath deepens the respirations, and causes a moderate acceleration of the pulmonary ventilation (*Speck*).

3. Impulses pass from the deglutition centre to the respiratory by what is termed "irradiation," and give rise to "deglutition-respiration," *i.e.*, to a feeble contraction of the diaphragm with each act of deglutition.

Section of both vagi causes **slower** and **deeper** respiratory movements, owing to the cutting off of those impulses which under normal conditions pass from the lungs to excite the respiratory centre (p. 814). [The inspirations are long and deep, and are followed by a short active expiration and a long pause (fig. 575). The effect may be studied by recording the respiratory movements with a stethograph, or by means of a sound placed in the œsophagus. Gad froze the vagi, and

thus set aside their activity—thus avoiding the stimulation inseparable from the act of dividing them—and observed that the effects were almost the same as those produced by their section.]

After section of both vagi, the **amount of air** taken in, and the CO_2 given off, however, are unchanged, but the inspiratory efforts are more vigorous and not so purposive (*Gad*). *Weak* tetanising currents applied to the *central* end of the vagus cause acceleration of the respirations, while, at the same time, the efforts of the respiratory muscles may be increased (fig. 576), or diminished, or remain unchanged

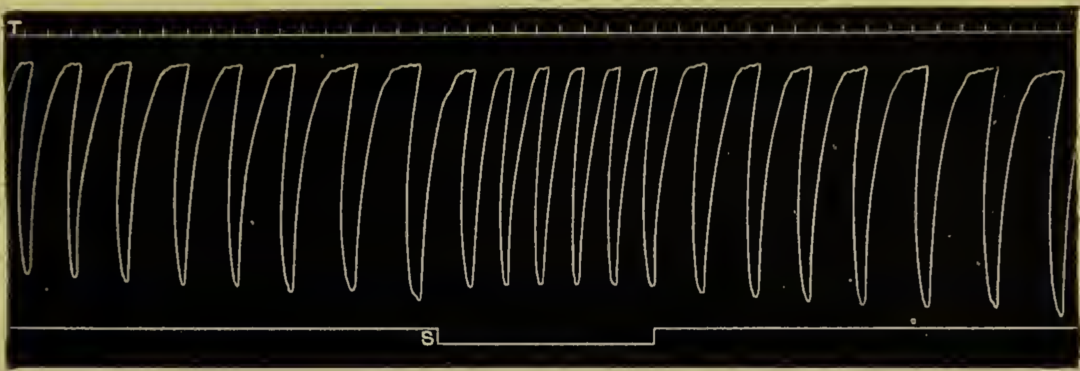


Fig. 576.

Effect of stimulating the central end of one vagus (rabbit) at S, with weak tetanising stimuli, both vagi being divided. The number of respirations is increased. T = time, *i.e.*, seconds (*Stirling*).

(*Gad*). [They may be increased in number and diminished in extent (*Stirling*, fig. 577).] *Strong* tetanising currents applied to the central end of the vagus may cause standstill of the respiration in the inspiratory phase (*Traube*) [*i.e.*, there is a

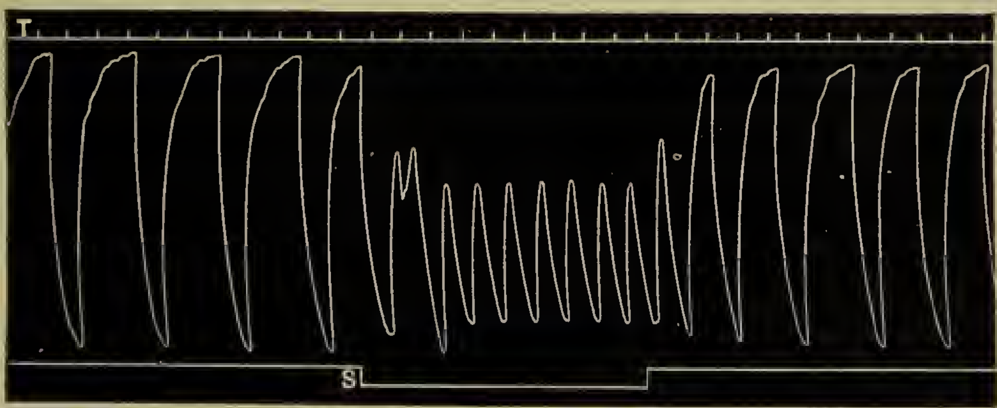


Fig. 577.

Effect of stimulating the central end of one vagus (rabbit) at S, both vagi being divided. T = time, *i.e.*, seconds (*Stirling*).

true tetanus of the diaphragm (fig. 579)], or especially in fatigue of the nerves, in the expiratory phase (fig. 578). *Single* induction shocks have no effect (*Marckwald and Kronecker*).

[The **inspiratory fibres**, which reflexly either accelerate the respirations or cause tetanus of the diaphragm in the inspiratory phase, run in the trunk of the vagus in the neck, and come from the lungs. These fibres are normally in action when the lungs are strongly diminished in volume, *e.g.*, at the end of each expiration, so that the contraction of the lung excites the next inspiratory act.]

[But the vagus in the neck also contains some **expiratory fibres**, *i.e.*, fibres whose excitation excites reflexly arrest of the respiration in the expiratory phase. They are not so numerous as the inspiratory fibres. Sometimes one succeeds, on stimulating the central end of the vagus, in causing reflexly a suspension of the

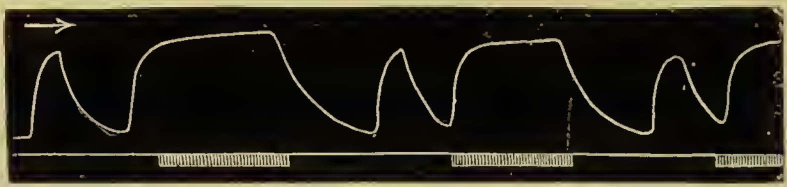


Fig. 578.

Respiratory tracing obtained by stimulation of the central end of the vagus in a chloralised rabbit. Arrest of the respiration in expiration.

contraction of the diaphragm and ribs, and consequently an arrest in the expiratory phase. Chloral diminishes the action of the inspiratory fibre, and allows the expiratory to manifest their action (*Fredericq*). In a rabbit poisoned with a large dose of chloral stimulation of the central end of the vagus is invariably followed

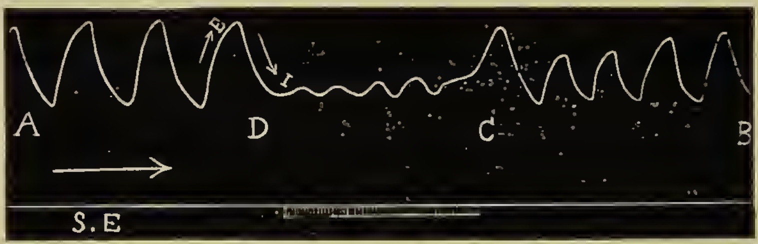


Fig. 579.

Effect of stimulating the central end of the vagus (rabbit). The respiratory movements are arrested in the inspiratory phase. Stimulation began at D and ended at C. E, expiration; I, inspiration.

by an arrest in expiration (fig. 578). These fibres are excited every time the lungs are distended, either by a normal inspiration or by insufflating the lungs artificially.]

[If the respiratory movements be arrested by stimulation of the central end of

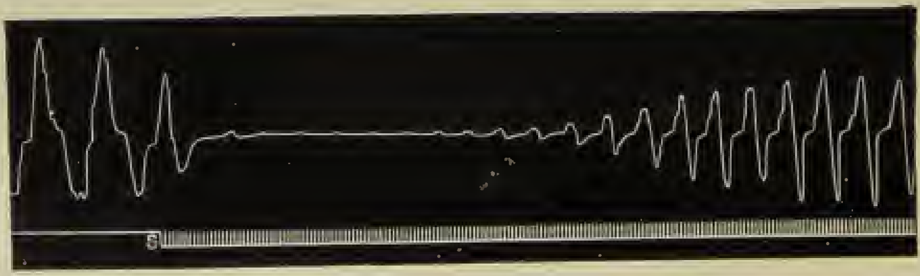


Fig. 580.

Respiratory movements of a rabbit arrested by stimulation of the central end of the vagus at S, but the movements begin and increase in spite of continuation of the stimulation (*Stirling*).

the vagus—both vagi being divided, the respirations, however, begin—at first small and feeble, and gradually gain, especially in frequency (fig. 580), and to a less degree in force in spite of continuation of the stimulation (*Stirling*).]

[Marckwald, while admitting that the respiratory centre is automatically active, as well as capable of being affected reflexly, comes to the conclusion, that, when the centre is separated from all nerve-channels by which afferent impulses can be conveyed to it, it is incapable of discharging rhythmical respiratory movements. He also asserts that the normal rhythmical respiration is a reflex act discharged chiefly through the vagi, and that the normal excitant of the respiratory centre is not dependent on the condition of the blood, either on the diminution of O, or the increase of CO_2. These results are opposed to the usually accepted view, and they are controverted by Loewy. Division of the medulla oblongata above the respiratory centre, so as to cut off all cerebral channels of communication, has very little effect on the respirations. If, after this, one or both vagi be divided there is—(1) an *extraordinary slowing* of the respiration ; the number of respirations may fall in the rabbit from 20 to 2 or 4 per minute ; (2) the rhythm is changed, in some cases the inspiration may be twice or thrice as long as the expiration, but, whatever the ratio of inspiration to expiration, the respiration is rhythmical ; (3) the *volume* of air respired is diminished (p. 819), but the volume for each respiration is deeper ; (4) the intra-thoracic pressure is increased during inspiration, and during expiration it is the same as before the vagotomy.]

	Before Vagotomy.				After Vagotomy.						
Experiment.	Intra-thoracic Pressure.	Frequency.	Volume Resp. per Min.	Volume Resp. per Respir.	Intra-thoracic Pressure.	Frequency.	Relation of Exp. Insp.	Volume Resp. per Min.	Diminution of Vol. per Min.	Volume Resp. per Respir.	Increase of Vol. for each Resp.
	mm.		c.cm.	c.cm.				c.cm.	%		%
1	− 30 to − 40	20	310–350	16	− 60 to − 70	4	½	130–140	59	33	100
2	− 22 to − 24	32	530–540	16	− 50 to − 60	2½	½	105–120	79·5	40	150

[The above table (from Loewy) shows the result. Loewy finds that, if the centre be separated from all centripetal channels, it still discharges respiratory movements, which are rhythmical, and he has shown that these rhythmical discharges are due to the condition of the blood.]

[If one lung be made atelectatic, *i.e.*, devoid of air, *e.g.*, by plugging its bronchus with a sponge-tent, then the pulmonary fibres of the vagus from this lung are no longer excited during respiration, and their section has no effect on the respiration. Section of the vagus on the sound side, however, has the same consequence as double vagotomy (*Loewy*).]

Wedenskii and Heidenhain find that a *temporary, weak*, electrical stimulus applied to the central end of the vagus, at the beginning of inspiration (rabbit), affects the depth of the succeeding inspirations, while a similar strong stimulus affects also the depth of the following expirations. If the stimulus be applied just at the commencement of expiration, stronger stimuli being required in this case, there is a diminution of the expiration and of the following inspiration. *Continued* tetanic stimulation of the vagus may cause decrease in the depth of the expirations, or at the same time alteration in the depth of the inspirations, without affecting the respiratory rhythm ; when the stimulation is *stronger*, inspiration and expiration are diminished with or without alteration of the frequency, and with the *strongest* stimuli, respirations cease either in the inspiratory or expiratory phase.

(*b*) The **inhibitory nerves** which affect the respiratory centre run in the superior laryngeal nerve (*Rosenthal*), and also in the inferior laryngeal nerve (*Pflüger and Burkart, Hering, Breuer*), to the respiratory centre (fig. 574 *inh*). [The superior laryngeal nerve is remarkable for containing a large number of inhibitory respiratory nerves, or nerves which cause arrest of the respiration in expiration, or even fibres causing expiration. One knows that it is the sensory nerve of the larynx, and that foreign bodies or irritating matter in the larynx excites coughing, *i.e.*, forced expiratory acts reflexly.]

According to Langendorff, direct electrical, mechanical, or chemical stimulation of the centre may arrest respiration, perhaps in consequence of the stimulus affecting the central ends of these inhibitory nerves where they enter the ganglia of the respiratory centre. During the reflex inhibition of the respiration in the expiratory phase, there is a suppression of the motor impulse in the inspiratory centre (*Wegele*).

Stimulation of the superior or inferior laryngeal nerves (*b*) or their *central* ends causes slowing, and even arrest of the respiration (in expiration—*Rosenthal*). Arrest of the respiration in expiration is also caused by stimulation of the nasal (*Hering and Kratschmer*) and ophthalmic branches of the trigeminus (*Christiani*),

of the olfactory, and glosso-pharyngeal (*Marckwald*). [Kratschmer found that tobacco-smoke blown into a rabbit's nostrils, or puffed through a hole in the trachea into the nose, by stimulating the nasal branch of the fifth nerve, arrested the respiration in the expiratory phase, while it had no effect when blown into the lungs. Ammonia vapour applied to the nostrils arrests it in the same way. If ammonia vapour be blown into the lungs (the nasal cavity being protected from its action), the respiration may be accelerated, or deepened, or arrested occasionally in expiration, *i.e.*, according to the fibres of the vagus acted on by the vapour in the lungs (*Knoll*). A stream of water dropped on a rabbit's nose will arrest the respirations in expiration for 10–20 secs., and in the duck the same means will arrest the respiration for 10 minutes (*Fredericq*). These reflex arrests of respiration obviously play a protective *rôle* for the animal.] Stimulation of the pulmonary branches of the vagus by breathing irritating gases (*Knoll*) causes standstill in expiration, although some other gases cause standstill in inspiration. Chemical stimulation of the trunk of the vagus,—by dilute solutions of sodic carbonate,—causes expiratory inhibition of the respiration; and mechanical stimulation,—rubbing with a glass rod,—inspiratory inhibition (*Knoll*). The stimulation of sensory cutaneous nerves,

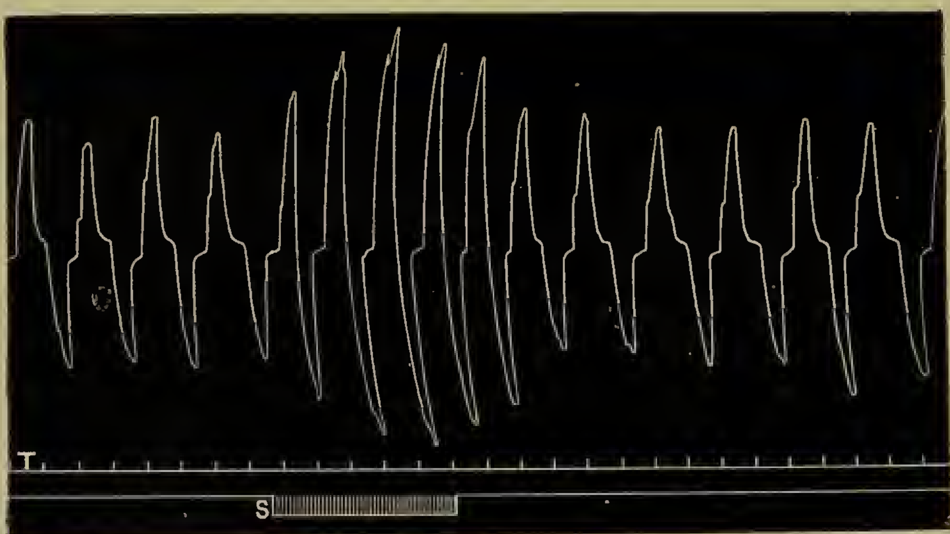


Fig. 581.

Effect on respiration of stimulation of central end of the sciatic nerve in the rabbit (*Stirling*).

especially of the chest and abdomen (as occurs on taking a cold douche), and stimulation of the splanchnics, cause standstill in expiration, the first cause often giving rise to temporary clonic contractions of the respiratory muscles. The respirations are often slowed to a very great extent by pressure upon the brain, [whether the pressure be due to a depressed fracture or effusion into the ventricles and subarachnoid space]. The respiration may be greatly oppressed and stertorous.

[All sensory nerves may act reflexly more or less like the vagus on the respiratory movements. Stimulation of the central end of the sciatic nerve usually accelerates the respiration (fig. 581), more rarely reflex expiratory arrest. The change may result in an increased number of respirations as well as increased depth.

If the respiratory movements and blood-pressure be recorded simultaneously, and a particular strength of stimulus applied to the central end of the sciatic nerve (rabbit), the blood-pressure is raised (fig. 582, B.P.), and the respirations may be increased in number but not raised in depth (fig. 582).]

The amount of work done by the respiratory muscles is altered during the reflex slowing of

the respiratory muscles, the work being increased during slow respiration, owing to the ineffectual inspiratory efforts (*Gad*). The volume of the gases which passes through the lungs during a given time remains unchanged (*Valentin*), and the gaseous exchanges are not altered at first (*Voit and Rauber*).

Automatic Regulation of Respiration.—Under normal circumstances, it would seem that the pulmonary branches of the vagus act upon the two respiratory centres, so as to set in action what has been termed the *self-adjusting* mechanism; thus, the inspiratory dilatation of the lungs stimulates mechanically the fibres which reflexly

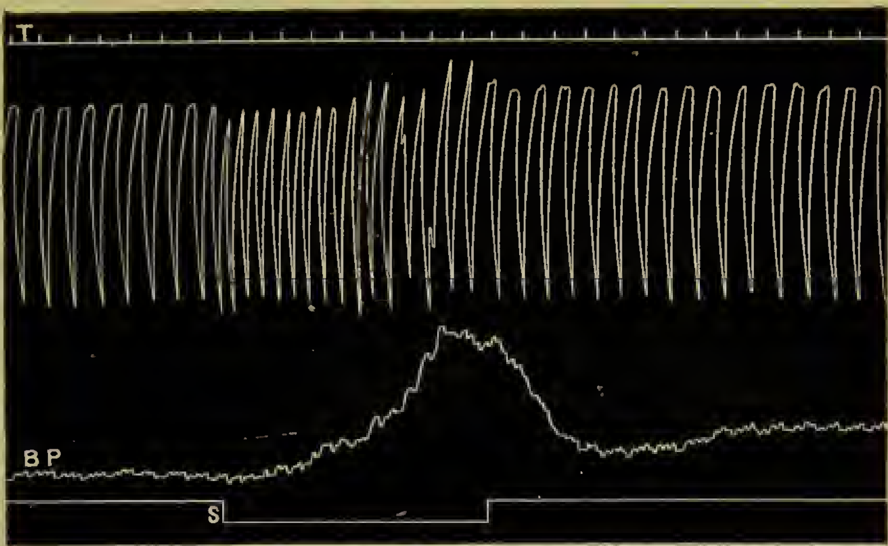


Fig. 582.

Effect of stimulation (S) of the central end of the sciatic nerve (rabbit) on the respirations and blood-pressure (B.P), (*Stirling*).

excite the *expiratory* centres, while the diminution of the lungs during expiration excites the nerves which proceed to the *inspiratory* centre (*Hering and Breuer, Head*). [Thus blowing into the lungs excites the act of expiration, and sucking air out of them excites inspiration.]

In this way we may explain the alternate play of inspiration and expiration. In deep narcosis, however, dilatation of the thorax in animals is followed first by cessation of the respiratory movements, and then by inspiration (*P. Guttmann*).

Discharge of the First Respiration.—The fœtus is in an apnœic condition until birth, when the umbilical cord is cut. During intrauterine life, O is freely supplied to it by the activity of the placenta. All conditions which interfere with this due supply of O, as compression of the umbilical vessels and prolonged labour pains, cause a decrease of the O and an increase of the CO_2 in the blood, so that the condition of the fœtal blood is so altered as to stimulate the respiratory centre, and thus the impulse is given for the discharge of the first respiratory movement (*Schwartz*). A fœtus, still within the unopened fœtal membranes, may make respiratory movements (*Vesalius*, 1542). If the exchange of gases be interrupted to a sufficient extent, dyspnœa and ultimately death of the fœtus may occur. If, however, the venous condition of the mother's blood develops very slowly, as in cases of quiet slow death of the mother, the medulla oblongata of the fœtus may gradually die without any respiratory movement being discharged (§ 324, 5).

According to this view, the respiratory movements are due to the direct action of the dyspnœic blood upon the medulla oblongata. [The excitability of the respiratory centre is less in the fœtus than in the newly born, and it increases from day to day after birth. Amongst the causes of the diminished excitability are the small amount of O in fœtal blood, and the slow velocity of the circulation. If an inspiration is discharged in the fœtus, it is at once arrested

by fluid passing into the nostrils and inhibiting the act reflexly. The chief cause of the first respiration after birth is undoubtedly the increasing venosity of the blood, and also the disappearance of the above-named reflex inhibitory process.] Death of the mother acts like compression of the umbilical cord. In the former case, the maternal venous blood robs the fœtal blood of its O, so that death of the fœtus occurs more rapidly (*Zuntz*). If the mother be *rapidly* poisoned with CO (§ 17), the fœtus may live longer, as the CO-hæmoglobin of the maternal blood cannot take any O from the fœtal blood (§ 16—*Hogyes*). In slow poisoning the CO passes into the fœtal blood (*Gréhant and Quinquand*).

In many cases, especially in cases of very prolonged labour, the excitability of the respiratory centre may be so diminished, that after birth the dyspnœic condition of the blood alone is not sufficient to excite respiration in a normal rhythmical manner. In such cases *stimulation* of the *skin* also acts, *e.g.*, partly by the cooling produced by the evaporation of the amniotic fluid from the skin. When air has entered the lungs by the first respiratory movements, the air within the lungs also excites the pulmonary branches of the vagus (*Pflüger*), and thus the respiratory centre is stimulated reflexly to increased activity. According to v. Preuschen's observations, stimulation of the cutaneous nerves is more effective than that of the pulmonary branches of the vagus. In animals which have been rendered apnœic by free ventilation of their lungs, respiratory movements may be discharged by strong cutaneous stimuli, *e.g.*, dashing on of cold water. The mechanical stimulation of the skin by friction or sharp blows, or the application of a cold douche, excites the respiratory centre. When the placental circulation is intact, cutaneous stimuli do not discharge respiratory movements (*Zuntz and Cohnstein*), (Artificial respiration, § 134).

[**Action of Drugs on the Respiratory Centre.**—Ammonia, salts of zinc and copper, strychnin, atropin, duboisin, apomorphin, emetin, the digitalis group, and heat increase the rapidity and depth of the respirations, while they become frequent and shallower after the use of alcohol, opium, chloral, chloroform, physostigmin. The excitability of the centre is first increased and then diminished by caffein, nicotin, quinine, and saponin (*Brunton*).]

369. CENTRE FOR THE INHIBITORY NERVES OF THE HEART—(CARDIO-INHIBITORY).

—The fibres of the **vagus**, when moderately stimulated, diminish the action of the heart; when strongly stimulated, however, they arrest its action and cause it to **stand still in diastole** (§ 352, 7); they are supplied to the vagus through the spinal accessory nerve, and have their centre in the medulla oblongata (§ 353).

[Gaskell has shown that stimulation of the vagus not only influences the rhythm of the heart's action, but modifies the other functions of the cardiac muscle. **Stimulation of the vagus** influences—(*a*) the *automatic rhythm*, *i.e.*, the rate at which the heart contracts automatically; (*b*) the *force* of the contractions, more especially the auricles, although in some animals, *e.g.*, the tortoise, the ventricles are not affected; (*c*) the *power of conduction*, *i.e.*, the capacity for conducting the muscular contractions. According to Gaskell, the vagus acts upon the rhythmical power of the muscular fibres of the heart.]

This centre may be excited **directly** in the medulla, and also **reflexly**, by stimulating certain afferent nerves.

Many observers assume that this centre is in a state of **tonic excitement**, *i.e.*, that there is a continuous, uninterrupted, regulating, and inhibitory action of this centre upon the heart through the fibres of the vagus. According to Bernstein, this tonic excitement is caused reflexly through the abdominal and cervical sympathetic.

I. Direct Stimulation of the Centre.—This centre may be stimulated **directly** by the same stimuli that act upon the respiratory centre. (1) *Sudden anæmia* of the oblongata, ligature of both carotids or both subclavians, or decapitating a rabbit, the vagi alone being left undivided, cause slowing and even temporary arrest of the action of the heart. (2) Sudden *venous hyperæmia* acts in a similar manner, *e.g.*, by ligaturing all the veins returning from the head. (3) *Increased venosity* of the blood, produced either by direct cessation of the respirations (rabbit), or by forcing into the lungs a quantity of air containing much CO_2 (*Traube*). As the circulation in the placenta (the respiratory organ of the fœtus) is interfered with during severe labour, this sufficiently explains the enfeeblement of the action of the heart which occurs during protracted labour; it is due to stimulation of

the central end of the vagus by the dyspnœic blood (*B. S. Schultze*). (4) At the moment the respiratory centre is excited, and an *inspiration* occurs, there is a variation in the inhibitory activity of the cardiac centre (*Donders*, *Pflüger*, *Fredericq*—§ 74, *a*, 4). (5) The centre is excited by increased *blood-pressure* within the cerebral arteries.

II. The centre may be excited **reflexly** by—(1) Stimulation of **sensory nerves** (*Lovèn*).

[This is illustrated in fig. 583, which shows the effect produced on the heart by stimulation of the central end of the infra-orbital nerve, at *c*. The heart movements were recorded by means of a needle inserted into the heart. The heart-beat was arrested for a moment and pulse-beats are much slower, and there is consequently a great fall of the blood-pressure.]

Fig. 583.

Fig. 583.—Momentary arrest and slowing of the heart-beat produced reflexly by stimulation of the central end of the infra-orbital nerve in the rabbit.

(2) Stimulation of the **central end of one vagus**, provided the other vagus is intact.

(3) Stimulation of the **sensory nerves of the intestines**, by tapping upon the belly (Goltz's **tapping experiment**), whereby the action of the heart is arrested. Stimulation of the splanchnic nerve directly (*Asp and Ludwig*), or of the abdominal or cervical sympathetic, produces the same result. Very strong stimulation of sensory nerves, however, arrests the above-named reflex effects upon the vagus (§ 361, 3).

Tapping Experiment.—Goltz's experiment succeeds at once, by tapping the intestines of a frog directly, say, with the handle of a scalpel, especially if the intestine has been exposed to the air for a short time, so as to become inflamed (*Tarchanoff*). Stimulation of the stomach of the dog causes slowing of the heart-beat (*Sig. Mayer and Pribram*). [M'William finds that the action of the heart of the eel may be arrested reflexly with very great facility. The reflex inhibition is obtained by slight stimulation of the gills (through the branchial nerves), the skin of the head and tail, and parietal peritoneum, by severe injury of almost any part of the animal, except the abdominal organs.]

[**Effect of Swallowing Fluids.**—Kronecker has shown that the act of swallowing interferes with or abolishes temporarily the cardio-inhibitory action of the vagus, so that the pulse-rate is greatly accelerated. Merely sipping a wineglassful of water may raise the rate 30 per cent. Hence, sipping cold water acts as a powerful cardiac stimulant.]

According to Hering, the excitability of the cardio-inhibitory centre is diminished by vigorous artificial ventilation of the lungs with atmospheric air. At the same time, there is a considerable fall of the blood-pressure (§ 352, 8, 4).

In man, a vigorous expiration, owing to the increased intra-pulmonary pressure, causes an acceleration of the heart-beat, which Sommerbrodt ascribes to a diminution of the activity of the vagi. At the same time the activity of the vaso-motor centre is diminished (§ 60, 2).

Stimulation of the trunk of the vagus at any point from the centre downwards, along its whole course, and also of certain of its cardiac branches [inferior cardiac,] causes the heart either to beat more slowly, or arrests its action in diastole. The result depends upon the strength of the stimulus employed; feeble stimuli slow the action of the heart, while strong stimuli **arrest it in diastole.** The **frog's heart** may be arrested by stimulating the fibres of the vagus upon the sinus venosus [or by stimulating the vagus in its course, as in fig. 584]. If *strong* stimuli be applied, either to the centre or to the course of the nerve, for a *long time*, the part stimulated becomes *fatigued* and the heart beats more rapidly in spite of the continued stimulation. If a part of the nerve lying nearer the heart be stimulated, inhibition of the heart's action is brought about, as the stimulus acts upon a fresh portion of nerve.

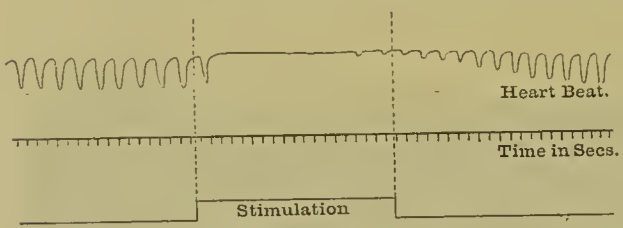


Fig. 584.

Beating of a frog's heart taken by means of a lever resting on the heart. The lowest curve shows when the vagus was stimulated and the consequent arrest of the heart-beat (*Stirling*).

[The action of the heart may be arrested by stimulation of the vagus, not only by means of electrical stimuli, but also by chemical (common salt, glycerin) or mechanical stimuli. As a rule, the right vagus is more powerful than the left. Suppose the heart to be arrested by stimulation of the vagus, the arrest is not permanent; in spite of continuation of the stimulation the heart begins to beat. At first the contractions are slower, and afterwards quicker. Fig. 585 shows the effect of stimulation of the vagus in a rabbit, the result being shown by recording the blood-pressure, and noting the sudden fall in the arterial pressure consequent on the arrest of the heart in diastole.]

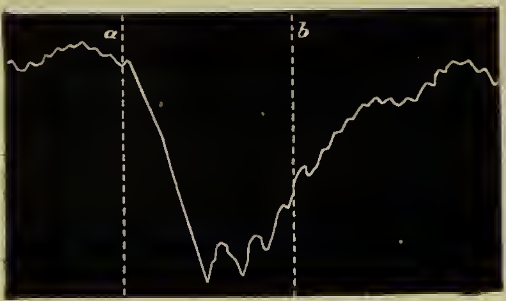


Fig. 585.

Blood-pressure tracing of the carotid artery of a rabbit. Effect of stimulation of the vagus (at *a*) causing a rapid fall of the blood-pressure (*Stirling*).

The following points have also been ascertained regarding the **stimulation of the inhibitory fibres** :—

1. The experiments of Löwit on the frog's heart, confirmed by Heidenhain, showed that electrical and chemical stimulation of the vagus produce different results, as regards the extent of the ventricular systole, as well as the number of heart-beats; the contractions either become smaller, or less frequent, or they become smaller and less frequent simultaneously. Strong stimuli cause, in addition, well-marked relaxation of the heart-muscle during diastole.

2. In order to cause inhibition of the heart, a *continuous* stimulus is not necessary. A *rhythmically interrupted* moderate stimulus suffices (*v. Bezold*); 18 to 20 stimuli per second are required for mammals, and 2 to 3 per second for cold-blooded animals.

3. Donders, with Prahl and Nüel, observed that arrest of the heart's action did not take place immediately the stimulus was applied to the vagus; but about $\frac{1}{6}$ of a second—period of latent stimulation—elapsed before the effect was produced on the heart.

4. If the heart be arrested by stimulation of the vagus, it can still contract, if it be excited *directly*, *e.g.*, by pricking it with a needle, when it executes a *single* contraction. [This holds good only for some animals, *e.g.*, frog, tortoise, birds and mammals. In fishes, only the ventricle responds to stimulation during marked inhibition; in the newt, only the bulbus

arteriosus. In the newt's heart, the sinus, auricles, and ventricle are all inexcitable to direct stimulation during strong inhibition.]

5. According to A. B. Meyer, inhibitory fibres are present only in the *right* vagus in the turtle. It is usually stated that the *right* vagus is more effective than the left in other animals, *e.g.*, rabbit (*Masoin*); but this is subject to many exceptions (*Landois and Langendorff*). [In the newt, the right vagus acts more readily on the ventricle than on the other parts of the heart; *slight* stimulation of the right vagus can arrest the ventricle, while the sinus and auricles go on beating.]

6. The vagus has been compressed by the finger in the neck of man (*Czermak, Concato*); but this experiment is accompanied by danger, and ought not to be undertaken. The electrotonic condition of the vagus is stated in § 335, III.

7. Schiff found that stimulation of the vagus of the frog caused acceleration of the heart-beat, when he displaced the blood of the heart with saline solution. If blood-serum be supplied to the heart, the vagus regains its inhibitory action.

8. Many **soda salts** in a proper concentration arrest the inhibitory action of the vagus, while **potash salts** restore the inhibitory function of the vagi suspended by the soda salts. If, however, the soda or potash salts act too long upon the heart, they produce a condition in which, after the inhibitory function of the vagi is abolished, it is not again restored. The heart's action in this condition is usually arhythmical (*Löwit*).

9. If the **intracardial pressure** be greatly increased, so as to accelerate greatly the cardiac pulsations, the activity of the vagus is correspondingly diminished (*J. M. Ludwig and Luchsinger*).

[**Differences in Animals.**—Perhaps the most remarkable fact in connection with the influence of the vagus on the eel's heart and that of all other **fishes** examined, is, that vagus-stimulation causes the sinus and auricle to be entirely inexcitable to direct stimulation during strong inhibition. Nerve-stimulation has in this case the very peculiar effect of rendering the muscular tissue temporarily incapable of responding to even the strongest direct stimuli, *e.g.*, powerful induction shocks. This would appear to be decisive evidence that the vagus acts on **muscle** directly, and not simply on automatic motor ganglia, as was held according to the old view (*M'William*).]

Poisons.—**Muscarin** stimulates the terminations of the vagus in the heart, and causes the heart to stand still in diastole (*Schmiedeberg and Koppe*). [See p. 99 for Gaskell's views.] If **atropin** be applied in solution to the heart, this action is set aside, and the heart begins to beat again. [Atropin abolishes completely the inhibitory action of the vagus on the heart. If it be injected into the jugular vein of a rabbit, the pulse-beats are increased 27 per cent., in the dog they may be trebled, and in a man under its full influence the pulse-beats may rise from 70 to 150 or more. After atropin, it is impossible to arrest the action of the heart by stimulation of the vagus, and in the frog this cannot be done even by stimulation of the inhibitory centre in the heart itself, so that atropin must be regarded as paralysing the *intracardiac terminations* of the vagus.] **Digitalin** diminishes the number of heart-beats by stimulating the cardio-inhibitory centre (vagus) in the medulla. Large doses diminish the excitability of the vagus centre, and increase at the same time the accelerating cardiac ganglia, so that the heart-beats are thereby increased. In small doses, digitalin raises the blood-pressure by stimulating the vaso-motor centre and the elements of the vascular wall (*Klug*). **Nicotin** first excites the vagus, then rapidly paralyses it. *Hydrocyanic acid* has the same effect (*Preyer*). *Atropin* (*v. Bezold*) and *curare* (large dose—*Cl. Bernard and Kölliker*) paralyse the vagi, and so does a very low temperature or high fever.

370. CENTRE FOR THE ACCELERATOR OR AUGMENTOR CARDIAC NERVES.—**Nervus Accelerans.**—It is more than probable that a centre exists in the medulla oblongata, which sends *accelerating fibres* to the heart. These fibres pass from the medulla oblongata—but from which part thereof has not been exactly ascertained—through the spinal cord, and leave the cord through the rami communicantes of several of the upper dorsal nerves, to pass into the sympathetic nerve. Some of these fibres, issuing from the spinal cord, pass through the first thoracic sympathetic ganglion and the ring of Vieussens, to join the cardiac plexus (figs. 586, 587). [These fibres, proceeding from the spinal cord, frequently accompany the nerve running along the vertebral artery], and they constitute the *Nervus accelerans cordis.* [Fig. 587 shows the accelerator fibres passing through the ganglion stellatum of the cat to join the cardiac plexus.]

[**Accelerans in the dog.**—These fibres leave the spinal cord as medullated fibres by the anterior roots of the second and third dorsal nerves, and it may be by the fourth and fifth nerves as well—pass *viâ* the white rami communicantes to the

second thoracic ganglion and ganglion stellatum—the latter is the first thoracic ganglion—and thence forwards through the annulus or ring of Vieussens to the inferior cervical ganglion. They then pass along the nerves arising either from the inferior cervical ganglion or one loop of the annulus of Vieussens. These emerging nerve-fibres are non-medullated, and as the augmentor fibres are medullated before they enter the sympathetic ganglia it is evident that they become non-medullated in these ganglia probably by ending in the multipolar nerve-cells of these ganglia, so that the emerging fibres may be regarded as continuous with the non-medullated processes of the sympathetic nerve-cells. They

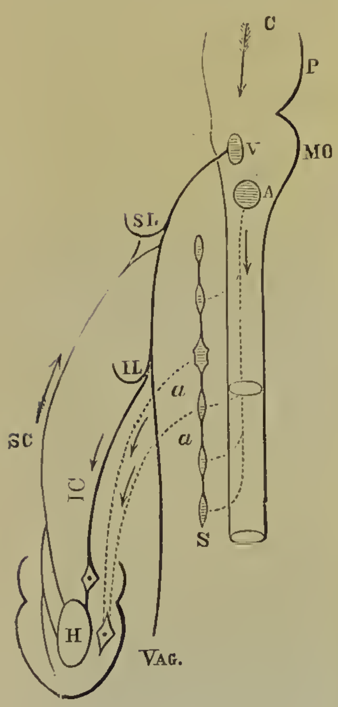


Fig. 586.

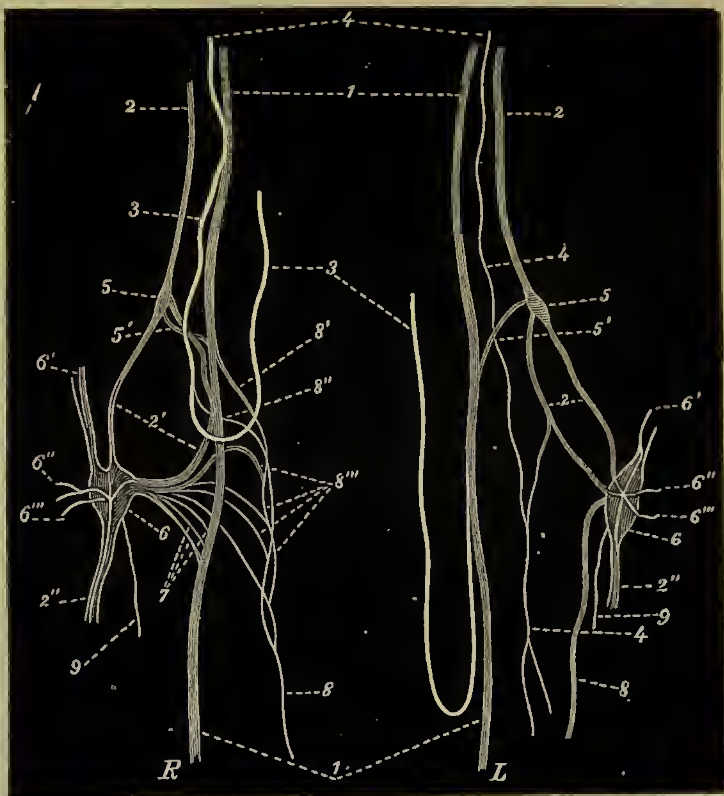


Fig. 587.

Fig. 586.—Scheme of the course of the accelerans fibres. P, pons; MO, medulla oblongata; C, spinal cord; V, inhibitory centre for heart; A, accelerans centre; VAG., vagus; SL, superior, IL, inferior laryngeal; SC, superior, IC, inferior cardiac; H, heart; C, cerebral impulse; S, cervical sympathetic; *a*, *a*, accelerans fibres. Fig. 587.—Cardiac plexus, and ganglion stellatum of the cat. R, right, L, left × 1½; 1, vagus; 2′ cervical sympathetic, and in the annulus of Vieussens; 2, communicating branches from the middle cervical ganglion and the ganglion stellatum; 2″, thoracic sympathetic; 3, recurrent laryngeal; 4, depressor nerve; 5, middle cervical ganglion; 5′, communication between 5 and the vagus; 6, ganglion stellatum (1st thoracic ganglion); 7, communicating branches with the vagus; 8, nervus accelerans; 8, 8′, 8″, roots of accelerans; 9, branch of the ganglion stellatum.

remain non-medullated from the ganglion to the heart. In this respect these fibres differ markedly from the inhibitory fibres of the vagus. The inhibitory fibres of the vagus, although they pass through ganglia, remain as fine medullated fibres all the way to the heart.]

[Stimulation of the accelerans nerve not only quickens the heart-beat and diminishes the diastole, but it increases its force, hence the term "augmentor" applied to it. It requires a pretty strong stimulus to excite it, and if the stimulation be kept up, the augmentor fibres are less easily exhausted than the inhibitory

fibres of the vagus. Prolonged stimulation of the nerve results in increased rapidity of the heart's action, and leads to a period of diminished energy on the part of the heart, the latter becoming exhausted. Thus this nerve may be regarded as the katabolic nerve of the heart, in opposition to the vagus, which is the anabolic nerve of the heart.]

If the vagi of an animal be divided, stimulation of the medulla oblongata, of the lower end of the divided cervical spinal cord, even of the lower cervical ganglion, or of the upper dorsal ganglion of the sympathetic (*Gang. stellatum*), causes acceleration of the heart-beats in the dog and rabbit, without the blood-pressure undergoing any change (*Cl. Bernard, v. Bezold, Cyon*).

[Fig. 588 shows the effect on the rate of the heart-beat—acceleration—by stimulation of the accelerans nerve in dog.]

Fig. 588.

Effect produced by stimulation of peripheral end of the accelerans cordis nerve. The heart beats quicker. Stimulation begun at S.

On stimulating the medulla oblongata or the cervical portion of the spinal cord, the *vaso-motor nerves* are, of course, simultaneously excited. The consequence is that the blood-vessels, supplied by vaso-motor nerves from the spot which is stimulated, contract, and the blood-pressure is greatly increased. Again, a simple increase of the blood-pressure accelerates the action of the heart; this experiment does not prove directly the existence of accelerating fibres lying in the upper part of the spinal cord. If, however, the splanchnic nerves be divided beforehand (when, as they supply the largest vaso-motor area in the body, the result of their division is to cause a great fall of the blood-pressure), then on stimulating the above-named parts, after this operation, the heart-beats are still increased in number, so that this increase cannot be due to the increased blood-pressure. Indirectly it may be shown, by dividing or extirpating all the nerves of the cardiac plexus, or at least all the nerves going to the heart, that stimulation of the medulla oblongata, or cervical part of the spinal cord, no longer causes an increased frequency of the heart's action to the same extent as before division of these nerves. The slightly increased frequency in this case is due to the increased blood-pressure.

The accelerating centre is certainly not continually in a state of *tonic* excitement, as section of the accelerans nerve does not cause slowing of the action of the heart; the same is true of destruction of the medulla oblongata or of the cervical spinal cord. In the latter case, the splanchnic nerves must be divided beforehand, to avoid the slowing effect on the action of the heart produced by the great fall of the blood-pressure consequent upon destruction of the cord, otherwise we might be apt to ascribe the result to the action of the accelerating centre, when it is in reality due to the diminished blood-pressure (*Cyon*).

According to the results of the older observers (*v. Bezold and others*), some accelerating fibres run in the *cervical sympathetic*. A few fibres pass through the vagus to reach the heart (§ 352, 7), and when they are stimulated, either the heart-beat is accelerated or the cardiac contractions strengthened (*Heidenhain and Löwit*), or the latter alone occurs (*Pawlow*). The inhibitory fibres of the vagus lose their excitability more readily than the accelerating fibres, but the vagus fibres are more excitable than those of the accelerans.

Tarchanoff has described some very rare cases of individuals who, by a merely *voluntary effort*, and while at rest, the respirations remaining unaffected, could nearly double the number of their pulse-beats.

Modifying Conditions.—When the peripheral end of the nervus accelerans is stimulated, a considerable time elapses before the effect upon the frequency of the heart takes place, *i.e.*, it has a **long latent period.** Further, the acceleration thus produced disappears gradually. If the vagus and accelerans fibres be stimulated **simultaneously**, only the inhibitory action of the vagus is manifested. If, *while the accelerans* is being stimulated, the vagus be suddenly excited, there is a prompt diminution in the number of the heart-beats; and if the stimulation of the vagus is stopped, the accelerating effect of the accelerans is again rapidly manifested (*C. Ludwig with Schmiedeberg, Bowditch, Baxt*). According to the experiments of Stricker and Wagner on dogs, with both vagi divided, a diminution of the number of the heart-beats occurred when both accelerantes were divided. This would indicate a tonic innervation of the latter nerves.

[**Accelerans in the Frog.**—Gaskell showed that stimulation of the vagus in the **frog** might produce two opposing effects: the one of the nature of inhibition, the other of augmentation. The augmentor fibres in the frog leave the cord by the anterior roots of the third spinal nerve, and by the ramus communicans of this nerve they pass into the third sympathetic ganglion, they run up through the second ganglion, and thence through the annulus of Vieussens to the first sympathetic ganglion, *i.e.*, the ganglion connected with the first spinal nerve. They then run up the short sympathetic nerve, enter the ganglion of the trunk of the vagus, pass through it and emerge, and are distributed with the vagus fibres, emerging from the ganglion trunci vagi. In the **crocodile**, the accelerans fibres leave the sympathetic chain at the large ganglion corresponding to the ganglion stellatum of the dog, and run along the vertebral artery up to the superior vena cava, and, after anastomosing with branches of the vagus, pass to the heart. "Stimulation of these fibres increases the *rate* of the cardiac rhythm, and augments the *force* of auricular contractions; while stimulation of the vagus slows the rhythm, and diminishes the strength of the auricular contractions." The *strength* of the *ventricular* contraction, both in the tortoise and crocodile, does not seem to be influenced by stimulation of the vagus, and probably also it is unaffected by the sympathetic. The so-called vagus of the frog, in reality, consists of pure vagus fibres and sympathetic fibres, and is in fact a vago-sympathetic. Gaskell finds that *stimulation of the sympathetic*, before it joins the combined ganglion of the sympathetic and vagus, produces *purely augmentor* or accelerating effects; while *stimulation of the vagus*, before it enters the ganglion, produces purely *inhibitory* effects. The two sets of fibres are quite distinct, so that in the **frog** the sympathetic is a purely augmentor (accelerator), and the vagus a purely inhibitory nerve. Acceleration is merely one of the effects produced by stimulation of these nerves; hence, Gaskell suggests that they ought to be called "**augmentor,**" or simply cardiac sympathetic nerves. The augmentor fibres are non-medullated in the trunk of the vagus, while the inhibitory fibres are medullated.]

[In his more recent researches Gaskell asserts that vagus stimulation produces *first* an inhibitory or depressing effect, but that it ultimately improves the condition of the heart as regards force, rate, or regularity—one or all of these. He regards it as a true **anabolic nerve** (§ 342, d).]

371. VASO-MOTOR CENTRE AND VASO-MOTOR NERVES.—**Vaso-motor Centre.**—The chief dominating or **general centre**, which supplies all the **non-striped muscles** of the arterial system with *motor* nerves (**vaso-motor**, vaso-constrictor, vaso-hypertonic nerves), lies in the medulla oblongata, at a spot which contains many ganglionic cells (*Ludwig and Thiry*). Those nerves which pass to the blood-vessels are known as **vaso-motor nerves.** The centre (which is 3 millimetres long and $1\frac{1}{2}$ millimetre broad in the rabbit) reaches from the region of the upper part of the floor of the medulla oblongata to within 4 to 5 mm. of the calamus scriptorius. Each half of the body has its own centre, placed $2\frac{1}{2}$ millimetres from the middle line on its own side, in that part of the medulla oblongata which represents the upward continuation of the lateral columns of the spinal cord;

according to Ludwig, Owsjannikow, and Dittmar, in the lower part of the superior olives. **Stimulation** of this central area causes contraction of all the arteries, and, in consequence, there is great increase of the arterial blood-pressure, resulting in swelling of the veins and heart. **Paralysis** of this centre causes relaxation and dilatation of all the arteries, and consequently there is an enormous fall of the blood-pressure. Under ordinary circumstances, the vaso-motor centre is in a condition of *moderate tonic* excitement (§ 366). Just as in the case of the cardiac and respiratory centres, the vaso-motor centre may be excited directly and reflexly.

[**Position—How ascertained.**—As stimulation of the *central* end of a sensory nerve, *e.g.*, the sciatic, in an animal under the influence of **curare**, causes a rise in the blood-pressure, even after removal of the cerebrum, it is evident that the centre is not in the cerebrum itself. For the effect of **chloral**, under the same conditions, see p. 833. By making a series of sections of the brain from above downwards, it is found that this reflex effect is not affected until a short distance above the medulla oblongata is reached. If more and more of the medulla oblongata be removed from above downwards, then the reflex rise of the blood-pressure becomes less and less, until, when the section is made 4 to 5 mm. above the calamus scriptorius, the reflex effect on the blood-pressure ceases altogether. This is taken to be the lower limit of the *general* vaso-motor centre. The bilateral centre corresponds to some large multipolar nerve-cells, described by Clarke as the antero-lateral nucleus.]

I. Direct Stimulation of the Centre.—The **amount** and **quality** of the **gases** contained in the **blood** flowing through the medulla are of primary importance. In the condition of apnœa (§ 368, 1), the centre seems to be very slightly excited, as the blood-pressure undergoes a considerable decrease. When the mixture of blood-gases is such as exists under normal circumstances, the centre is in a state of moderate excitement, and running parallel with the respiratory movements are variations in the excitement of the centre (Traube-Hering curves—§ 85), these variations being indicated by the rise of the blood-pressure. When the blood is highly venous, produced either by asphyxia or by the inspiration of air containing a large amount of CO_2, the centre is strongly excited, so that all the arteries of the body contract, while the venous system and the heart become distended with blood (*Thiry*). At the same time, the velocity of the blood-stream is increased (*Heidenhain*). The same result is produced by ligature of both the carotid and subclavian arteries, thus causing sudden anæmia of the medulla oblongata; and, no doubt, also by the sudden stagnation of the blood in venous hyperæmia.

Emptiness of the Arteries after Death.—The venosity of the blood which occurs after death always produces an energetic stimulation of the vaso-motor centre, in consequence of which the arteries are firmly contracted. The blood is thereby forced towards the capillaries and veins, and thus is explained the "emptiness of the arteries after death."

Effect on Hæmorrhage.—Blood flows much more freely from large wounds, when the vaso-motor centre is intact, than if it be destroyed (frog). As psychical excitement undoubtedly influences the vaso-motor centre, we may thus explain the influence of psychical excitement (speaking, &c.) upon the cessation of hæmorrhage. If the hæmorrhage be severe, stimulation of the medulla oblongata, due to the anæmia, may ultimately cause constriction of the small arteries, and thus arrest the bleeding. Thus, surgeons are acquainted with the fact that dangerous hæmorrhage is often arrested as soon as unconsciousness, due to cerebral anæmia, occurs. If the heart be ligatured in a frog, all the blood is ultimately forced into the veins, and this result is also due to the anæmic stimulation of the oblongata (*Goltz*). In *mammals*, when the heart is ligatured, the equilibration of the blood-pressure between the arterial and venous systems takes place more slowly when the medulla oblongata is destroyed than when it is intact (*v. Bezold, Gscheidlen*).

[**Effect of Destruction of the Vaso-motor Centre.**—If two frogs be pithed and their hearts exposed, and both be suspended, then the hearts of both will be found to beat rhythmically and fill with blood. Destroy the medulla oblongata and spinal cord of one of them, then immediately in this case, the heart, although continuing to beat with an altered rhythm, ceases to be filled with blood; it appears collapsed, pale, and bloodless. There is a great accumulation of the blood in the abdominal organs and veins, and it is not returned to the heart, so that the

arteries are empty. This experiment of Goltz is held to show the existence of *venous tonus* depending on a cerebro-spinal centre. If a limb of this frog be amputated, there is little or no hæmorrhage, while in the other frog the hæmorrhage is severe. The bearing of this experiment on conditions of "shock" is evident.]

Action of Poisons.—*Strychnin* stimulates the centre directly, even in curarised dogs, and so do *nicotin* and *Calabar bean*.

Direct Electrical Stimulation.—On stimulating the centre directly in animals, it is found that single induction shocks only become effective when they succeed each other at the rate of 2 to 3 shocks per second. Thus there is a "**summation**" of the single shocks. The maximum contraction of the arteries, as expressed by the maximum blood-pressure, is reached when 10 to 12 *strong*, or 20 to 25 *moderately* strong, shocks per second are applied (*Kronecker and Nicolaides*).

Course of the Vaso-motor Nerves.—From the vaso-motor centre fibres proceed directly through some of the cranial nerves to their area of distribution; through the trigeminus partly to the interior of the **eye** (§ 347, I., 2), through the lingual and hypoglossal to the **tongue** (§ 347, III., 4), through the vagus to a limited extent to the **lungs** (frog) (§ 352, 8, 2), [the vaso-motor fibres pass to the lungs from the anterior roots of the 2nd to the 7th upper dorsal nerves in the dog (§ 356)], and to the **intestines** *viâ* the splanchnics (§ 352, 11).

All the other vaso-motor nerves descend in the lateral columns of the spinal cord (§ 364, 9); hence, stimulation of the lower cut end of the spinal cord causes contraction of the blood-vessels supplied by the nerves below the point of section (*Pflüger*). In their course through the cord these fibres form connections with the *subordinate vaso-motor centres in the grey matter of the cord* (§ 362, 7), and then leave the cord either directly through the *anterior* roots of the spinal nerves to their areas of distribution, or pass through the rami communicantes into the sympathetic, and from them reach the blood-vessels to which they are distributed (§ 356) [see fig. 530].

The following is the arrangement of these nerves in the region of the **head**:—The *cervical portion of the sympathetic* supplies the great majority of the blood-vessels of the head (see *Sympathetic*, § 356, A, 3). In some animals, the *great auricular nerve* supplies a few vaso-motor fibres to its own area of distribution (*Schiff, Lovèn, Moreau*). The vaso-motor nerves to the **upper extremities** pass through the anterior roots of the middle dorsal nerves into the thoracic sympathetic, and upwards to the 1st thoracic ganglion, and from thence through the rami communicantes to the brachial plexus (*Schiff, Cyon*). The skin of the **trunk** receives its vaso-motor nerves through the dorsal and lumbar nerves. The vaso-motor nerves to the **lower extremities** pass through the nerves of the lumbar and sacral plexuses into the sympathetic, and from thence to the lower limbs (*Pflüger, Schiff, Cl. Bernard*). The **lungs** are supplied from the dorsal spinal cord through the 1st thoracic ganglion (*Brown-Séquard, Fick and Badoud, Lichtheim*). [In the dog fibres come through the 2nd to the 7th dorsal nerves.] It is said that in the frog the vaso-motor nerves to the lungs pass by the vagus (*Coureur*). The **splanchnic** is the greatest vaso-motor nerve in the body, and supplies the **abdominal viscera** (§ 356, B—*v. Bezold, Ludwig and Cyon*). The vaso-motor nerves of the **liver** (§ 173, 6), **kidney** (§ 276), and **spleen** (§ 103) have been referred to already. According to Stricker, most of the vaso-motor nerves leave the spinal cord between the 5th cervical and the 1st dorsal vertebræ. [Gaskell finds that in the dog (fig. 439) they begin to leave the cord at the 2nd dorsal nerve (§ 366), and the great outflow of vaso-motor nerves is between the 2nd dorsal and the 2nd lumbar nerves in the dog.]

As a general rule, the blood-vessels for the **skin** of the trunk and extremities are innervated from those nerves which give other fibres (*e.g.*, sensory) to those regions. The different vascular areas behave differently with regard to the intensity of the action of the vaso-motor nerves. The most powerful vaso-motor nerves are those that act upon the blood-vessels of peripheral parts, *e.g.*, the toes, the fingers, and

ears; while those that act upon central parts seem to be less active (*Lewaschew*), *e.g.*, on the pulmonic circulation (§ 88).

II. Reflex Stimulation of the Centre.—There are fibres contained in the different afferent nerves, whose stimulation affects the vaso-motor centre. There are nerve-fibres whose stimulation *excites* the vaso-motor centre, thus causing a stronger contraction of the arteries, and consequently an increase of the arterial blood-pressure. These are called "**pressor**" fibres. Conversely, there are other fibres whose stimulation reflexly diminishes the excitability of the vaso-motor centre. These act as reflex inhibitory nerves on the centre, and are known as "**depressor**" fibres.

Pressor, or excito-vaso-motor nerves, have already been referred to in connection with the superior and inferior laryngeal nerves (§ 352, 12, *a*), in the trigeminus, which, when stimulated directly (§ 347), causes a pressor action, as well as when stimulating vapours are blown into the nostrils (*Hering and Kratschmer*). [The

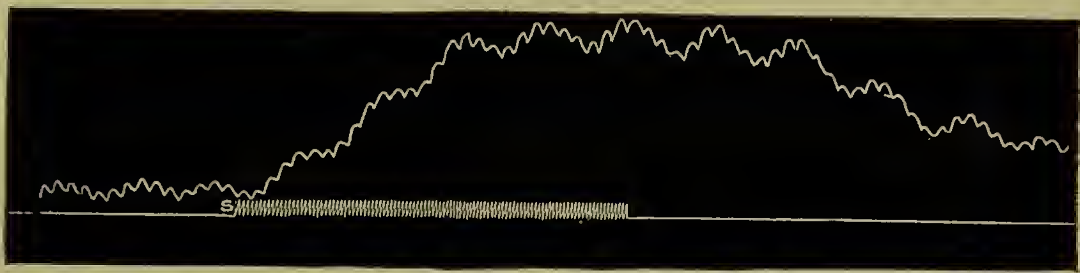


Fig. 589.

Fig. 589.—Effect on the blood-pressure in carotid, produced by stimulation of the central end of the sciatic nerve in the rabbit. Stimulation began at S.

rise of the blood-pressure in this case, however, is accompanied by a change in the character of the heart's beat and in the respirations. Rutherford has shown that in the rabbit the vapour of chloroform, ether, amyl nitrite, acetic acid, or ammonia held before the nose of a rabbit greatly retards or even arrests the heart's action, and the same is true if the nostrils be closed by the hand. This arrest does not occur if the trachea be opened, and Rutherford regards the result as due not to the stimulation of the sensory fibres of the trigeminus, but to the *state of the blood* acting on the cardio-inhibitory nerve apparatus.] Hubert and Roever found pressor fibres in the cervical sympathetic; S. Mayer and Pribram found that mechanical stimulation of the stomach, especially of its serosa, caused pressor effects (§ 352, 12, *c*]. According to Lovén, the *first* effect of stimulating every sensory nerve is a pressor action.

[If a dog be poisoned with **curare**, and the *central* end of one sciatic nerve be stimulated, there is a great and steady rise of the blood-pressure, chiefly owing to the contraction of the abdominal blood-vessels, and at the same time there is no change in the heart-beat (fig. 589). If, however, the animal be poisoned with **chloral**, there is a fall of the blood-pressure resembling a depressor effect.]

[The effect of the vaso-motor nerves on the blood-vessels, and consequently on the blood-pressure, may be illustrated by the following experiment. In a curarised dog artificial respiration is kept up, and a blood-pressure taken by means of the kymograph. Fig. 590, 1, gives the tracing obtained, which may be taken as normal. The spinal cord is then divided transversely at the level of the atlas, with the result that there is a sudden fall of the blood-pressure (fig. 590, 2), equal to 5 cm. of Hg. This is due to dilatation of the small arteries previously kept in a state of tonus by the vaso-motor nerves. The latter are now divided, the blood-vessels dilate, and therefore the blood-pressure falls. At the same time the tem-

perature of superficial parts rises, because they contain more blood. Suppose the peripheral end of the divided cord to be faradised, besides contraction of the muscles of the body generally, the vaso-motor nerves are stimulated; there is consequent contraction, especially of the small arteries, resulting in a rise of the blood-pressure (fig. 590, 3), and a fall of temperature in the superficial parts. The rise of the blood-pressure takes place gradually, and remains at a certain level (equal in this experiment to 9 cm. Hg). At 4 the stimulation ceases, and after a short period the pressure falls (fig. 590, 5), and continues to fall until it is lower at the outset of the experiment (fig. 590, 1)

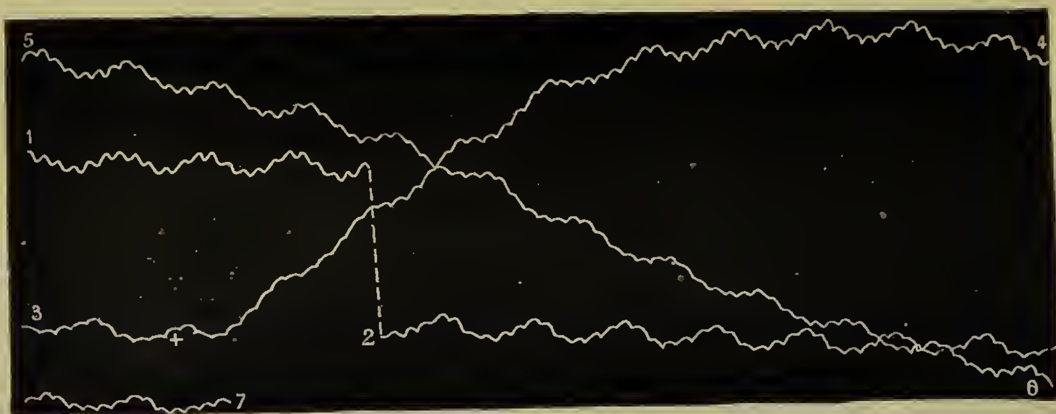


Fig. 590.

1, Normal blood-pressure tracing in a dog. 2, Fall of the blood-pressure after section of the bulb. 3, (+), faradic stimulation of the peripheral end of the divided cord. 5, Return and subsequent fall of the blood-pressure after cessation of the stimulation.

O. Naumann found that **weak**, electrical stimulation of the skin caused at first contraction of the blood-vessels, especially of the mesentery, lungs, and the web, with simultaneous excitement of the cardiac activity and acceleration of the circulation (frog). **Strong** stimuli, however, had an opposite effect, *i.e.*, a depressor effect, with simultaneous decrease of the cardiac activity. Grützner and Heidenhain found that **contact with the skin** caused a pressor effect, while painful impressions produced no effect. The application of **heat** and **cold** to the skin produces reflexly a change in the lumen of the blood-vessels and in the cardiac activity (*Röhrig*, *Winternitz*). Pinching the skin causes contraction of the vessels of the pia mater of the rabbit (*Schüller*), and the same result was produced by a warm bath, while cold dilated the vessels. These results are due partly to pressor and partly to depressor effects, but the chief cause of the dilatation of the blood-vessels is the increased blood-pressure due to the cold constricting the cutaneous vessels. Heat, of course, has the opposite effect. In **man**, most stimuli applied to sensory nerves, produce an effect:—feeble cutaneous stimuli, tickling (even unpleasant odours, bitter or acid tastes, optical and acoustic stimuli) at the part where they are applied, cause a fall of the cutaneous temperature, and diminution of the volume of the corresponding limb, sometimes increase of the general blood-pressure and change of the heart-beat. The opposite effects are produced by painful stimulation, the action of heat (and even by pleasant odours and sweet tastes). The former cause simultaneously dilatation of the cerebral vessels and increase the vascular contents of the skull,—the latter cause the opposite results (*Istomanow and Tarchanoff*).

Depressor fibres, *i.e.*, fibres whose stimulation diminishes the activity of the vaso-motor centre, are present in many nerves. They are specially numerous in the **superior cardiac** branch of the vagus, which is known as the **depressor nerve** (§ 352, 6). [When the central end of the depressor nerve is stimulated in the rabbit, after a rather long latent period there is a steady fall of the blood-pressure. This is due to the afferent impulses passing up the depressor nerve and through the vagus to the vaso-motor centre in the bulb. The vaso-motor action of the bulb is thereby diminished, so that there is dilatation of the blood-vessels, especially of the splanchnic area of blood-vessels in the abdomen, and this great dilatation of

blood-vessels in the abdomen is consequently followed by a steady and marked fall of the blood-pressure (fig. 591).]

The trunk of the vagus below the origin of the depressor also contains other depressor fibres (*v. Bezold*), as well as the pulmonary fibres (dog). The latter also act as depressors, during strong expiratory efforts (§ 74). Moreover, Hering found that inflating the lungs (to 50 mm. Hg pressure) caused a fall of the blood-pressure (and also accelerated the heart-beats—§ 369, II). Stimulation of the central end of sensory nerves, especially when it is intense and long continued, causes dilatation of the blood-vessels in the area supplied by them (*Lovèn*). According to Latschenberger and Deahna, all sensory nerves contain both pressor and depressor fibres.

[If a rabbit be poisoned with curare, and the *central* end of the **great auricular nerve** be stimulated, there is a double effect—one local and the other general; the blood-vessels throughout the body, but especially in the splanchnic area, contract,

Fig. 591.

Fall of the blood-pressure in the carotid of a rabbit produced by stimulation of the depressor nerve (*Stirling*).

so that there is a general rise of the blood-pressure, while the blood-vessels of the ear are dilated. If the central end of the **tibial nerve** be stimulated, there is a rise of the general blood-pressure, but a local dilatation of the saphena artery in the limb of that side (*Lovèn*). Again, the temperature of one hand and the condition of its blood-vessels influence that of the other. If one hand be dipped in cold water, the temperature of the other hand falls. Thus, pressor and depressor effects may be obtained from the same nerve. The vaso-motor centre, therefore, primarily regulates the condition of the blood-vessels, but through them it obtains its importance by regulating and controlling the *blood-supply* according to the needs of an organ.]

The central artery of a rabbit's ear contracts regularly and rhythmically 3 to 5 times per minute. Schiff observed that stimulation of sensory nerves caused a dilatation of the artery, which was preceded by a slight temporary constriction.

Depressor effects are produced in the area of an artery on which direct pressure is made, as occurs, for example, when the sphygmograph is applied for a long time—the pulse-curves become larger, and there are signs of diminished arterial tension (§ 75).

Rhythmical Contraction of Arteries.—In the intact body slow alternating contraction and dilatation, without a uniform rhythm, have been observed in the arteries of the ear of the rabbit, the membrane of a bat's wing, and the web of a frog's foot. This arrangement, observed by Schiff, supplies more or less blood to the parts, according to the action of external conditions. It has been called a "**periodic regulatory vascular movement.**" This movement may be useful when a vessel is occluded, as after ligature, and may help to establish more rapidly the collateral circulation. Stefani has shown that this occurs with more difficulty after section of the nerves.

Direct, local applications may influence the lumen of the blood-vessels; **cold** and **moderate electrical stimuli** cause **contraction**; while, conversely, **heat** and **strong**

mechanical or **electrical stimuli** cause **dilatation**, although with the last two there is usually a preliminary constriction.

Drugs.—Almost all the digitalis group of substances cause constriction; quinine and salicin constrict the splenic vessels. The other febrifuges dilate the vessels (*Thomson*). See p. 110.

Effect on Temperature.—The vaso-motor nerves influence the temperature, not only of individual parts, but of the whole body.

1. **Local Effects.**—**Section** of a peripheral vaso-motor nerve, *e.g.*, the **cervical sympathetic**, is followed by dilatation of the blood-vessels of the parts supplied by it (such as the ear of the rabbit), the intra-arterial pressure dilating the paralysed walls of the vessels. Much arterial blood, therefore, passes into and causes *congestion* and redness of the parts, or hyperæmia, while, at the same time, the **temperature** is increased. There is also increased transudation through the dilated capillaries within the dilated areas; the velocity of the blood-stream is of course diminished, and the blood-pressure increased. The pulse is also felt more easily, because the blood-vessels are dilated. Owing to the increase of the blood-stream, the blood may flow from the veins almost arterial (bright red) in its characters, and the pulse may even be propagated into the veins, so that the blood spouts from them (*Cl. Bernard*). **Stimulation** of the peripheral end of a vaso-motor nerve causes the opposite results—pallor, owing to contraction of the vessels, diminished transudation, and fall of the temperature on the surface. The smaller arteries may contract so much that their lumen is almost obliterated. Continued stimulation ultimately exhausts the nerve, and causes at the same time the phenomena of paralysis of the vascular wall.

Secondary results.—The immediate results of paralysis of the vaso-motor nerves lead to other effects; the paralysis of the muscles of the blood-vessels must lead to congestion of the blood in the part; the blood moves more slowly, so that the parts in contact with the air cool more easily, and hence the first stage of *increase* of the temperature may be followed by a *fall* of the temperature. The ear of a rabbit with the sympathetic divided, after several weeks becomes cooler than the ear on the sound one. If in man the motor muscular nerves, as well as the vaso-motor fibres, are paralysed, then the paralysed limb becomes cooler, because the paralysed muscles no longer contract to aid in the production of heat (§ 338), and also because the dilatation of the muscular arteries, which accompanies a muscular contraction, is absent. Should atrophy of the paralysed muscles set in, the blood-vessels also become smaller. Hence, paralysed limbs in man generally become cooler as time goes on. The *primary* effect, however, in a limb, *e.g.*, after section of the sciatic or lesion of the brachial plexus, is an increase of the temperature.

If, at the same time, the vaso-motor nerves of a large area of the skin be paralysed, *e.g.*, the lower half of the body after section of the spinal cord, then so much heat is given off from the dilated blood-vessels that either the warming of the skin lasts for a very short time and to a slight degree, or there may be cooling at once. Some observers (*Tschetschichin*, *Naunyn*, *Quincke*) have recorded a rise of the temperature after section of the cervical spinal cord, but Riegel did not observe this increase.

2. **Effect on the Temperature of the Body.**—Stimulation or paralysis of the vaso-motor nerves of a *small* area has practically no effect on the general temperature of the body. If, however, the vaso-motor nerves of a *considerable area* of the skin be suddenly paralysed, then the temperature of the entire body falls, because more heat is given off from the dilated vessels than under normal circumstances. This occurs when the spinal cord is divided high up in the neck. The inhalation of a few drops of amyl nitrite, which dilates the blood-vessels of the skin, causes a fall of the temperature (*Sassetzki and Manassein*). Conversely, stimulation of the vaso-motor nerves of a large area increases the temperature, because the constricted vessels give off less heat. The temperature in fever may be partly explained in this way (§ 220, 4).

The **activity of the heart**, *i.e.*, the number and energy of the cardiac con-

tractions, is influenced by the condition of the vaso-motor nerves. When a large vaso-motor area is paralysed, the blood-channels are dilated, so that the blood does not flow to the heart at the usual rate and in the usual amount, as the pressure is considerably diminished. Hence, the heart executes extremely small and feeble contractions. Stricker observed that the heart of a dog ceased to beat on extirpating the spinal cord from the 1st cervical to the 8th dorsal vertebra. Conversely, we know that stimulation of a large vaso-motor area, by constricting the blood-vessels, raises the arterial blood-pressure considerably. As the arterial pressure affects the pressure within the left ventricle, it may act as a mechanical stimulus to the cardiac wall, and increase the cardiac contractions both in number and strength. Hence, the circulation is accelerated (*Heidenhain, Slavjansky*).

Splanchnic Area.—By far the largest vaso-motor area in the body is that controlled by the splanchnic nerves, as they supply the blood-vessels of the abdomen (§ 161); hence, stimulation of their peripheral ends is followed by a great rise of the blood-pressure. When they are divided, there is such a fall of the blood-pressure that other parts of the body become more or less anæmic, and the animal may even die from "being bled into its own belly," *i.e.*, from what has been called "**intravascular hæmorrhage.**" Animals whose portal vein is ligatured die for the same reason (*C. Ludwig and Thiry*) [see § 87]. The capacity of the vascular system, depending as it does in part upon the condition of the vaso-motor nerves, influences the *body-weight*. Stimulation of certain vascular areas may cause the rapid excretion of water, and we may thus account in part for the diminution of the body-weight which has been sometimes observed after an epileptic attack terminating with polyuria.

Trophic Disturbances sometimes occur after affections of the vaso-motor nerves (§ 343, II., *c*) Paralysis of the vaso-motor nerves not only causes dilatation of the blood-vessels and local increase of the blood-pressure, but it may also cause increased transudation through the capillaries [§ 203]. When the active contraction of the muscles is abolished, the blood-stream at the same time becomes slower, and in some cases the skin becomes livid, owing to the venous congestion. There is a diminution of the normal transpiration, and the epidermis may be dry and peel off in scales. The growth of the hair and nails may be affected by the congestion of blood, and other tissues may also suffer.

Vaso-motor Centres in the Spinal Cord. — Besides the dominating centre in the medulla oblongata, the blood-vessels are acted upon by *local* or *subordinate vaso-motor centres in the grey matter of the spinal cord*, as is proved by the following observations:—If the spinal cord of an animal be divided, then all the blood-vessels supplied by vaso-motor nerves below the point of section are paralysed as the vaso-motor fibres proceed from the medulla oblongata. If the animal lives, the blood-vessels regain their tone and their former calibre, while the rhythmical movements of their muscular walls are ascribed to the subordinate centres in the lower part of the spinal cord (*Lister, Goltz*—§ 362, 7).

The **subordinate spinal centres** may, further, be stimulated **directly** by dyspnœic blood, and also **reflexly**, in the rabbit and frog (*Ustimowitsch*). After destruction of the medulla oblongata, the arteries of the frog's web still contract reflexly when the sensory nerves of the hind leg are stimulated (*Putnam, Nussbaum, Vulpian*). In the dog, opposite the 3rd to 6th dorsal nerve is a spinal vaso-motor centre (origin of the splanchnic), which can be excited reflexly (*Smirnow*), and there is a similar one in the lower part of the spinal cord (*Vulpian*).

If the lower divided part of the cord be *crushed*, the blood-vessels again dilate, owing to the destruction of the subordinate centres. In animals which survive this operation, the vessels of the paralysed parts gradually recover their normal diameter and rhythmical movements. This effect is ascribed to *ganglia*, which are supposed to exist along the course of the vessels. [It is to be recollected that the existence of these peripheral nervous mechanisms has not been proved.] These ganglia [or peripheral nervous mechanisms] might be compared to the ganglia of the heart, and seem by themselves capable of sustaining the movements of the

vascular wall. Even the blood-vessels of an excised kidney exhibit periodic variations of their calibre (*C. Ludwig and Mosso*). It is important to observe that the walls of the blood-vessels contract as soon as the blood becomes highly *venous*. Hence, the blood-vessels offer a greater resistance to the passage of venous than of arterial blood (*C. Ludwig*). Nevertheless, the blood-vessels, although they recover part of their tone and mobility, never do so *completely*.

The effects of direct mechanical, chemical, and electrical stimuli on blood-vessels may be due to their action on these peripheral nervous mechanisms. The arteries may contract so much as almost to disappear, but sometimes dilatation follows the primary stimulus.

Lewaschew found that limbs, in which the vaso-motor fibres had undergone degeneration, reacted like intact limbs to variations of temperature; heat relaxed the vessels, and cold constricted them. It is, however, doubtful if the variations of the vascular lumen depend upon the stimulation of the peripheral nervous mechanisms. Amyl nitrite and digitalis are supposed to act on those hypothetical mechanisms.

The **pulsating veins** in the bat's wing still continue to beat after section of all their nerves, which is in favour of the existence of local peripheral nervous mechanisms (*Luchsinger, Schiff*).

Influence of the Cerebrum.—The cerebrum influences the vaso-motor centre, as is proved by the sudden pallor that accompanies some psychical conditions, such as fright or terror. There is a centre in the grey matter of the cerebrum where stimulation causes cooling of the opposite side of the body.

Although there is one general vaso-motor centre in the medulla oblongata, which influences *all* the blood-vessels of the body, it is really a *complex composite* centre, consisting of a *number* of closely aggregated centres, each of which presides over a particular vascular area. We know something, *e.g.*, of the *hepatic* (§ 175) and *renal* centres (§ 276).

Many **poisons** excite the vaso-motor nerves, such as ergotin, tannic acid, copaiba, and cubebs others *first excite*, and then paralyse, *e.g.*, chloral hydrate, morphia, laudanosin, veratrin, nicotin, Calabar bean, alcohol; others rapidly *paralyse* them, *e.g.*, amyl nitrite, CO (§ 17), atropin, muscarin. The paralytic action of the poison is proved by the fact that, after section of the vagi and accelerantes, neither the pressor nor the depressor nerves, when stimulated, produce any effect. Many pathological infective agents affect the vaso-motor nerves.

The **veins** are also influenced by vaso-motor nerves, and so are the **lymphatics**, but we know very little about this condition.

[**Tonus of the Portal Vein.**—The portal vein is certainly supplied by many nerve-fibres (*Mall*), and it seems to be endowed with a marked tonus, for it is capable of accommodating itself either to a very large or a very small quantity of blood, in fact it can diminish its capacity tenfold (*Kronecker*).]

Pathological.—The **angio-neuroses**, or nervous affections of blood-vessels, form a most important group of diseases. The parts primarily affected may be either the peripheral nervous mechanisms, the subordinate centres in the cord, the dominating centre in the medulla, or the grey matter of the cerebrum. The effect may be direct or reflex. The dilatation of the vessels may also be due to stimulation of vaso-dilator nerves, and the physician must be careful to distinguish whether the result is due to paralysis of the vaso-constrictor nerves or stimulation of the vaso-dilator fibres.

Angio-neurosis of the skin occur in affections of the vaso-motor nerves, either as a diffuse redness or pallor; or there may be **circumscribed** affections. Sometimes, owing to the stimulation of individual vaso-motor nerves, there are local cutaneous arterio-spasms (*Nothnagel*). In certain acute febrile attacks—after previous initial violent stimulation of the vaso-motor nerves, especially during the cold stage of fever—there may be different forms of paralytic phenomena of the cutaneous vessels. In some cases of epilepsy in man, Trousseau observed irregular, red, angio-paralytic patches (**tâches cérébrales**). Continued strong stimulation may lead to interruption of the circulation, which may result in gangrene of the skin and deeper-seated parts (*Weiss*).

Hemicrania, due to unilateral spasm of the branches of the carotid on the head, is accompanied by severe headache (*Du Bois-Reymond*). The cervical sympathetic nerve is intensely stimulated—a pale, collapsed, and cool side of the face, contraction of the temporal artery like a firm whip-cord, dilatation of the pupil, secretion of thick saliva, are sure signs of this affection. This form may be followed by the opposite condition of paralysis of the cervical sympathetic, where the effects are reversed. Sometimes the two conditions may alternate.

Basedow's disease is a remarkable condition, in which the vaso-motor nerves are concerned; the heart beats very rapidly (90 to 129–200 beats per minute), causing palpitation; there is

swelling of the thyroid gland (**struma**), and projection of the eyeballs (**exophthalmos**), with imperfectly co-ordinated movements of the upper eyelid, whereby the plane of vision is raised or lowered. Perhaps in this disease we have to deal with a simultaneous stimulation of the accelerans cordis (§ 370), the motor fibres of Müller's muscles of the orbit and eyelids (§ 347, I.), as well as of the vaso-dilators of the thyroid gland. The disease may be due to direct stimulation of the sympathetic channels or their spinal origins, or it may be referred to some reflex cause. It has also been explained, however, thus, that the exophthalmos and struma are the consequence of vaso-motor paralysis, which results in enlargement of the blood-vessels, while the increased cardiac action is a sign of the diminished or arrested inhibitory action of the vagus. All these phenomena may be caused, according to Filehne, by injury to the upper part of both restiform bodies in rabbits.

Visceral Angio-neuroses.—The occurrence of sudden hyperæmia with transudations and ecchymoses in some thoracic or abdominal organs may have a neurotic basis. As already mentioned, injury to the pons, corpus striatum, and optic thalamus may give rise to hyperæmia, and ecchymoses in the lungs, pleuræ, intestines, and kidneys. According to Brown-Séquard, compression or section of one-half of the pons causes ecchymoses, especially in the lung of the opposite side; he also observed ecchymoses in the renal capsule after injury of the lumbar portion of the spinal cord (§ 379).

The dependence of **diabetes mellitus** upon injury to the vaso-motor nerves is referred to in § 175; the action of the vaso-motor nerves on the **secretion of urine** in § 276; and **fever** in § 220.

372. VASO-DILATOR CENTRE AND NERVES.—Although a **vaso-dilator centre** has not been definitely proved to exist in the medulla, still its existence there has been surmised. Its action is opposed to that of the vaso-motor centre. The centre is certainly not in a continuous or tonic state of excitement. The vaso-dilator nerves behave in their functions similarly to the cardiac branches of the vagus; both, when stimulated, cause relaxation and rest (*Schiff, Cl. Bernard*). Hence, these nerves have been called **vaso-inhibitory**, vaso-hypotonic, or **vaso-dilator nerves**. Dyspnœic blood stimulates this centre as well as the vaso-motor centre, so that the cutaneous vessels are dilated, while simultaneously the vessels of the internal organs are contracted and the organs anæmic, owing to the stimulation of their vaso-motor centre (*Dastre and Morat*). Nicotin is a powerful excitant of the vaso-dilator nerves (*Ostroumoff*); it raises the temperature of the foot (dog), and increases the formation of lymph (*Rogowicz*).

[The **existence of vaso-dilator nerves** is assumed in accordance with such facts as the following:—If the **chorda tympani** be divided, there is no change in the blood-vessels of the sub-maxillary gland; but if its *peripheral* end be stimulated, in addition to other results (§ 145), there is dilatation of the blood-vessels of the sub-maxillary gland, so that the veins of this gland discharge bright florid blood, and, indeed, the vein may spout like an artery. Similarly, if the **nervi erigentes** be divided, there is no effect on the blood-vessels of the penis (§ 362, 4); but if their *peripheral* ends be stimulated with Faradic electricity, the sinuses of the corpora cavernosa dilate, become filled with blood, and erection takes place (§ 436). Other examples in **muscle** and elsewhere are referred to below.]

Course of the Vaso-dilator Nerves.—To some organs they pass as special nerves—to other parts of the body, however, they proceed along with the vaso-motor and other nerves. According to Dastre and Morat, the vaso-dilator nerves for the **bucco-labial region** (dog) pass out from the cord by the 1st to the 3rd dorsal nerves, and go through the rami communicantes into the sympathetic, then to the superior cervical ganglion, and lastly through the carotid and inter-carotid plexus into the trigeminus. [The fibres occur in the posterior segment of the ring of Vieussens, and if they be stimulated there is dilatation of the vessels in the lip and cheek on that side. The maxillary branch of the trigeminus, however, also contains vaso-dilator fibres proper to itself (*Laffont*). In the grey matter of the cord there is a special subordinate centre for the vaso-dilator fibres of the bucco-labial region. This centre may be acted on reflexly by stimulation of the vagus, especially its pulmonary branches, and even by stimulating the sciatic nerve. The **ear** receives its nerves from the 1st dorsal and lowest cervical ganglion, the **upper limb** from the thoracic portion, and the **lower limb** from the abdominal portion of the sympathetic. The vaso-dilator fibres run to the **sub-maxillary** and **sub-lingual glands**, and also to the anterior part of the **tongue** in the **chorda tympani** (§ 349, 4), while those for the posterior part of the **tongue** run in the glosso-pharyngeal nerve (§ 351, 4—*Vulpian*).

The vaso-dilator fibres for the **kidneys** are contained chiefly in the lower dorsal and upper lumbar nerves (§ 276). *Stimulation* of the **nervi erigentes** proceeding from the sacral plexus causes dilatation of the arteries of the **penis**, together with congestion of the corpora cavernosa (§ 436) (*Eckhard, Lovén*). Eckhard found that erection of the penis can be produced by stimulation of the spinal cord and of the pons as far as the peduncles, which may explain the phenomenon of priapism in connection with pathological irritations in these regions. The **muscles** receive the vaso-dilator fibres for their vessels through the trunks of the motor nerves. *Stimulation of a motor* nerve or the spinal cord causes not only contraction of the corresponding muscles, but also dilatation of their blood-vessels (§ 294, II.—*C. Ludwig and Sczelkow, Hafix, Gaskell*)—the dilatation of the vessels taking place even when the muscle is prevented from shortening. [Gaskell observed under the microscope the dilatation produced by stimulation of the nerve to the mylohyoid muscle of the frog.] The vaso-dilator nerve-fibres remain medullated up to their terminal ganglion (*Gaskell*).

The **vaso-dilators** (like the vaso-motors, p. 837) also have **subordinate centres** in the **spinal cord**, *e.g.*, the fibres of the labio-buccal region at the 1st to 3rd dorsal vertebræ. This centre may be influenced reflexly through the pulmonary fibres of the vagus, and also through the sciatic (*Laffont, Smirnow*). According to Holtz, a similar centre lies in the lowest part of the cord, which may be affected reflexly through the nerves of the intestines (*Pal*).

Goltz showed that, in the **nerves to the limbs** (*e.g.*, in the sciatic nerve or nerves of the brachial plexus), the vaso-motor and vaso-dilator fibres lie side by side in the same nerve. If the peripheral end of the sciatic nerve be stimulated immediately after it is divided, the action of the vaso-constrictor fibres overcomes that of the dilators. If the peripheral end be stimulated 4 to 6 days after the section, when the vaso-constrictors have lost their excitability, the blood-vessels dilate under the action of the vaso-dilator fibres. *Stimuli, which are applied at long intervals to the nerve, act especially on the vaso-dilator fibres; while tetanising stimuli act on the vaso-motors. The latent period of the vaso-dilators is longer, and they are more easily exhausted than the vaso-motors* (*Bowditch and Warren*). The sciatic nerve receives both kinds of fibres from the sympathetic. It is assumed that the peripheral nervous mechanisms in connection with the blood-vessels are influenced by both kinds of vascular nerves; the vaso-motors (constrictors) increase, while the vaso-dilators diminish the activity of these mechanisms or ganglia. [It is, however, possible to explain their effects by supposing that they act directly upon the muscular fibres of the blood-vessels, without the intervention of any nervous ganglionic structures.]

[The vaso-dilator fibres arise within the central nervous system, but they present a marked contrast to the vaso-constrictor fibres in many respects, some of which have already been stated. While the vaso-constrictors arise from a limited but extensive area of the cord (§ 356), the vaso-dilators, at least so far as they have been investigated, are said to arise from a wide area, which, unlike that of the vaso-constrictors, is not limited chiefly to the thoracic region of the cord, but on the contrary, there is a copious outflow of these nerve-fibres from the cranial and sacral regions of the central nervous system. In fact, it would seem that vaso-dilator fibres arise from all parts of the spinal cord. As to the course of these fibres, it is to be noted that in several respects this differs from that of the vaso-constrictors. As already stated, the latter consist of fine medullated fibres (1·8 μ to 3·5 μ) which become non-medullated in the ganglia of the sympathetic system. The vaso-dilators, however, appear to follow a more direct course—and they also are fine medullated fibres as they leave the cord by the anterior roots—but they present this difference, that they run as medullated fibres to the organs in which they are distributed, where they become non-medullated.]

[Section of the spinal cord high up in the neck causes, of course, a great fall of the blood-pressure, owing to the division of the vaso-motor nerves. In the dog the pressure may fall to 30–40 mm. Hg. After isolation of the cord, in rabbits alone, stimulation of the central end of a sensory nerve causes a rise of the blood-pressure; in dogs, however, under the same conditions, the blood-pressure *falls*. Dyspnœic blood also causes a rise of the blood-pressure, which

is preceded by a fall (*Ustimowitch*). This reflex fall of the blood-pressure takes place after section of the splanchnics, and the nerves to the extremities, but it does not take place if the spinal cord be divided at the lumbar or lower dorsal region. If the cord be divided in the lower dorsal region stimulation of the brachial plexus has no effect, while the fall occurs after stimulation of the central end of the sciatic. These experiments indicate that the vaso-dilator nerves which cause the fall of the blood-pressure arise in the lower part of the spinal cord (lumbar), and that they are probably contained in the visceral nerves and not in those for the extremities (*Thayer and Pal*).]

In the muscles of the face, paralysed by extirpation of the facial nerve, stimulation of the ring of Vieussens causes **pseudo-motor** contractions of these muscles, just as stimulation of the chorda tympani causes such contractions in the paralysed tongue (§ 349, 4), after section of the hypoglossal nerve (*Rogowicz*).

In analysing the vascular phenomena resulting from experiments on these nerves, we must be very careful to determine whether the dilatation is the result of *stimulation of the vaso-dilators*, or a consequence of paralysis of the vaso-constrictors. *Psychical* conditions act upon the vaso-dilator nerves—the blush of shame, which is not confined to the face, but may even extend over the whole skin, is probably due to stimulation of the vaso-dilator centre.

Influence on Temperature.—The vaso-dilator nerves obviously have a considerable influence on the *temperature* of the body and on the heat of the individual parts of tbo body. *Both* vascular centres must act as important regulatory mechanisms for the radiation of heat through the cutaneous vessels (§ 214, II.). Probably they are kept in activity reflexly by sensory nerves. Disturbances in their function may lead to an abnormal accumulation of heat, as in fever (§ 220), or to abnormal cooling (§ 213, 7). Some observers, however, assume the existence of an intracranial "**heat-regulating centre**" (*Tschetschichin*, *Naunyn*, *Quincke*). According to Wood, separation of the medulla oblongata from the pons causes an increased radiation and a diminished production of heat, due to the cutting off of the influences from the heat-regulating centre (§ 377).

373. SPASM-CENTRE — SWEAT-CENTRE. — Spasm-Centre. — In the medulla oblongata, just where it joins the pons, there is a centre, whose stimulation causes *general spasms*. The centre may be excited by suddenly producing a highly venous condition of the blood ("**asphyxia spasms**"), in cases of drowning in mammals (but not in frogs), sudden **anæmia** of the medulla oblongata, either in consequence of hæmorrhage or ligature of both carotids and subclavians (*Kussmaul and Tenner*), and lastly, by sudden venous stagnation caused by compressing the veins coming from the head. In all these cases, the stimulation of the centre is due to the sudden *interruption of the normal exchange of the gases*. When these factors act quite gradually, death may take place without convulsions. Direct stimulation by means of *chemical* substances (ammonia carbonate, potash, and soda salts, &c.) applied to the medulla, quickly causes general convulsions (*Papellier*). Intense direct *mechanical* stimulation of the medulla, as by its sudden destruction, causes general convulsions.

Position.—Nothnagel attempted by direct stimulation to map out the position of the spasm-centre in rabbits; it extends from the area above the ala cinerea upwards to the corpora quadrigemina. It is limited externally by the locus cœruleus and the tuberculum acusticum. In the frog, it lies in the lower half of the 4th ventricle (*Heubel*). The centre is affected in extensive reflex spasms (§ 364, 6), *e.g.*, in poisoning with strychnin and in hydrophobia.

Drugs.—Many inorganic and organic poisons, most cardiac poisons, nicotin, picrotoxin, ammonia (§ 277), and the compounds of barium cause death after producing convulsions, by acting on the spasm-centre (*Röber*, *Heubel*, *Böhm*).

If the arteries going to the brain be ligatured so as to paralyse the medulla oblongata, then, on ligaturing the abdominal aorta, spasms of the lower limbs occur, owing to the anæmic stimulation of the motor ganglia of the spinal cord (*Sigm. Mayer*).

Pathological—Epilepsy.—Schröeder van der Kolk found the blood-vessels of the oblongata dilated and increased in cases of epilepsy. Brown-Séquard observed that injury to the central or peripheral nervous system (spinal cord, oblongata, peduncle, corpora quadrigemina, sciatic nerve) of guinea-pigs produced epilepsy, and this condition even became *hereditary*. Stimulation of the cheek or of the face, "**epileptic zone,**" on the same side as the injury (spinal cord), caused at once an attack of epilepsy; but when the peduncle was injured, the opposite side must be stimulated. Westphal made guinea-pigs epileptic by repeated light blows on the skull, and this condition also became hereditary. In these cases there was effusion of blood in the medulla

oblongata and upper part of the spinal cord (§§ 375 and 378, I.). Direct stimulation of the cerebrum also produces epileptic convulsions. Strong electrical stimulation of the motor areas of the cortex cerebri is often followed by an epileptic attack (§ 375). [It is no unfrequent occurrence while one is stimulating electrically the motor areas of the cortex cerebri of a dog, to find the animal exhibiting symptoms of local or general epilepsy.]

Sweat-Centre.—A **dominating centre** for the secretion of the sweat of the entire surface of the body (§ 289, II.)—with subordinate spinal centres (§ 362, 8)—occurs in the medulla oblongata (*Adamkiewicz, Marmé, Nawrocki*). It is double, and in rare cases the excitability is unequal on the two sides, as is manifested by unilateral perspiration (§ 289, 2).

[**Drugs.**—Calabar bean, nicotin, picrotoxin, camphor, and ammonium acetate, cause a secretion of sweat by acting directly on the sweat-centre. Muscarin causes local stimulation of the peripheral sweat-fibres—it causes sweating of the hind limbs after section of the sciatic nerves. Atropin arrests the action of muscarin (*Ott, Wood, Field, Nawrocki*).]

[**Regeneration of the Spinal Cord.**—In some animals, true nervous matter is reproduced after part of the spinal cord has been destroyed, at least this is so in tritons and lizards (*H. Müller*). In these animals, when the tail is removed, it is reproduced, and Müller found that a part of the spinal cord corresponding to the new part of the tail is reproduced. Morphologically, the elements were the same, but the spinal nerves were not reproduced, while physiologically, the new nerve-substance was not functionally active ; it corresponds, as it were, to a lower stage of development. According to Masius and Vanlair, an excised portion of the spinal cord of a frog is reproduced after six months ; while Brown-Séquard maintains that re-union of the divided surfaces of the cord takes place in pigeons after six to fifteen months. A partial re-union is asserted to occur in dogs by Dentan, Naunyn, and Eichhorst, although Schieferdecker obtained only negative results, the divided ends being united only by connective-tissue (*Schwalbe*).]

374. PSYCHICAL FUNCTIONS OF THE BRAIN.—The hemispheres of the cerebrum are usually said to be the *seat of all the psychical activities.* Only when they are intact are the processes of thinking, feeling, and willing possible. After they are destroyed, the organism comes to be like a complicated machine, and its whole activity is only the expression of the external and internal stimuli which act upon it. The psychical activities appear to be located in both hemispheres, so that after destruction of a considerable part of one of them, the other seems to act in place of the part destroyed. [Objection has been taken to the term the "seat of" the will and intelligence, and undoubtedly it is more consistent with what we know, or rather do *not* know, to say, that the existence of volition and intelligence is dependent on the connection of the cerebral cortex with the rest of the brain.]

[That a certain condition of the cerebral hemispheres is necessary for the manifestation of the intellectual faculties is admitted on all hands; for compression of the brain, *e.g.*, by a depressed fracture of the skull, and sudden cessation of the supply of blood to the brain, abolish consciousness. The intellectual faculties are affected by inflammation of the meninges involving the surface of the brain, the action of drugs affects the intellectual and other faculties; but while all this is admitted we cannot say precisely upon what parts of the brain ideation depends.]

[The **pre-frontal area,** or the convolutions in front of the ascending frontal supplied by the anterior cerebral artery, are sometimes regarded as the anatomical substratum of certain mental acts. At any rate, electrical stimulation of these parts is not followed by muscular motion, and, according to Ferrier, if this region be extirpated in the monkey, there is no motor or sensory disturbance in this animal ; it still exhibits emotional feeling, all its special senses remain, and the power of voluntary motion is retained ; but, nevertheless, there is a decided alteration in the animal's character and behaviour, so that it exhibits considerable psychological alterations, and, according to Ferrier, "it has lost to all appearance the faculty of attention and intelligent observation."]

Observations on Man.—Cases in which considerable *unilateral* lesions or destruction of one hemisphere have taken place, without the psychical activities *appearing* to suffer, sometimes occur. The following is a case communicated by Longet :—A boy, 16 years of age, had his parietal bone fractured by a stone falling on it, so that part of the protruding brain-matter had to be removed. On reapplying the bandages, more brain-matter had to be removed. After 18 days he fell out of bed, and more brain-matter protruded, which was removed. On the 35th day he got intoxicated, tore off the bandages, and with them a part of the brain-matter. After

his recovery the boy still retained his intelligence, but he was hemiplegic. Even when *both* hemispheres are *moderately* destroyed, the intelligence *appears* to be intact; thus, Trousseau describes the case of an officer whose fore-brain was pierced transversely by a bullet. There was *scarcely* any appearance of his mental or bodily faculties being affected. In other cases, destruction of parts of the brain peculiarly alters the character. We must be extremely careful, however, in forming conclusions in all such cases. [In the celebrated "**American crow-bar case**" recorded by Bigelow, a young man was hit by a bar of iron 1¼ inch in diameter, which traversed the anterior part of the left hemisphere, going clean out at the top of his head. This man lived for thirteen years without any permanent alterations of motor or sensory functions; but "the man's disposition and character were observed to have undergone a serious change. There were, however, some changes which might be referable to injury to the frontal region." In all cases it is most important to know both the exact *site* and the *extent* of the lesion. Ross points out that the characteristic features of lesions in the pre-frontal cortical region are afforded by "psychical disturbances, consisting of dementia, apathy, and somnolency."]

Imperfect development of the cerebrum.—**Microcephalia** and hydrocephalus yield every result between diminution of the psychical activities and idiocy. Extensive inflammation, degeneration, pressure, anæmia of the blood-vessels, and the actions of many poisons produce the same effect.

Flourens' Doctrine.—Flourens assumed that the **whole of the cerebrum** is concerned in *every* psychical process. From his experiments on pigeons, he concluded that if a small part of the hemispheres remained intact, it was sufficient for the manifestation of the mental functions; just in proportion as the grey matter of the hemispheres is removed, *all* the functions of the cerebrum are enfeebled, and when all the grey matter is removed all the functions are abolished. According to this view, neither the different faculties nor the different perceptions are localised in special areas. Goltz holds a somewhat similar view to that of Flourens. He assumes that if an uninjured part of the cerebrum remain, it can to a certain extent perform the functions of the parts that have been removed. This Vulpian has called the law of "**functional substitution**" (loi de suppléance).

The **phrenological doctrine** of Gall († 1828) and Spurzheim assumes that the different mental faculties are located in different parts of the brain, and it is assumed that a large development of a particular organ may be detected by examining the external configuration of the head (**Cranioscopy**).

Removal of the Cerebrum.—After the removal of both cerebral hemispheres, in most animals, every voluntary movement and consciousness of impressions and sensory perception and signs of intelligent volition appear to cease. On the other hand, the whole mechanical movements and the maintenance of the equilibrium of the movements are retained. The **maintenance of the equilibrium** depends upon the mid-brain, and is regulated by important reflex channels (§ 379).

Sudden cessation of the circulation in the brain, *e.g.*, by decapitation, is followed at once by cessation of the mental faculties. When Hayem and Barrier perfused the blood of a horse through the carotids of a decapitated dog's head, the head showed signs of consciousness for 10 seconds, but not longer.

The **mid-brain** (corpora quadrigemina) is connected not only with the grey matter of the spinal cord and medulla oblongata, the seat of extensive reflex mechanisms (§ 367), but it also receives fibres coming from the higher organs of sense, which also excite movements reflexly. The corpora quadrigemina are also supposed to contain a reflex inhibitory apparatus (§ 361, 2). The joint action of all these parts makes the corpora quadrigemina one of the most important organs for the harmonious execution of movements, and this even in a higher degree than the medulla oblongata itself (*Goltz*). Animals with their corpora quadrigemina intact retain the equilibrium of their bodies under the most varied conditions, but they lose this power as soon as the mid-brain is destroyed (*Goltz*). Christiani locates the co-ordinating centre for the change of place and the maintenance of the equilibrium, in mammals, in front of the inspiratory centre in the 3rd ventricle (§ 368).

That **impressions from the skin** and **sense-organs** are concerned in the **maintenance of the equilibrium** is proved by the following facts:—A frog without its cerebrum at once loses its power of balancing itself as soon as the skin is removed from its hind limbs. The action of impressions communicated through the eyes is proved by the difficulty or impossibility of maintaining the equilibrium in

nystagmus (§ 350), and by the vertigo which often accompanies paralysis of the external ocular muscles. In persons whose cutaneous sensibility is diminished, the eyes are the chief organs for the maintenance of the equilibrium; they fall over when the eyes are closed. [This is well illustrated in cases of locomotor ataxia (p. 795).]

Frog without cerebrum.—A frog with its cerebrum or cerebral ganglia (fig. 592, 1) removed retains its power of maintaining its equilibrium. It can sit, spring, or execute complicated co-ordinated movements when appropriate stimuli are applied; when placed on its back, it immediately turns into its normal position on its belly; if stimulated it gives one or two springs, and then comes to rest; when thrown into water, it swims to the margin of the vessel, and it may crawl up the side, and sit passive upon the edge of the vessel. When incited to move, it exhibits the most complete harmony and unity in all its movements. Unless it is stimulated, it does not make independent, voluntary, purposive movements. It continues to sit in the same place, it takes no food, it shows no symptoms of fear, and ultimately, if left alone, it becomes desiccated like a mummy on the spot where

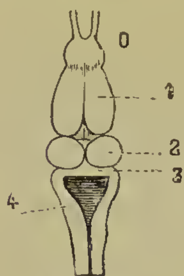


Fig. 592.

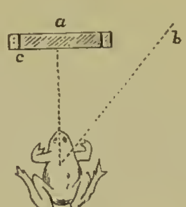


Fig. 593.

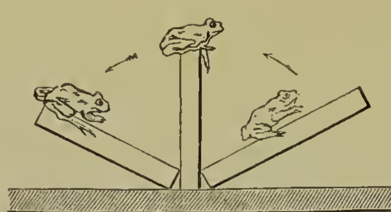


Fig. 594.

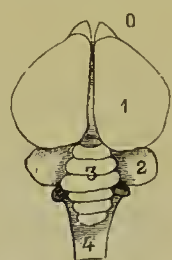


Fig. 595.

Fig. 592.—Brain of the frog seen from above. O, olfactory lobe; 1, cerebral hemispheres; 2, optic lobes; 3, cerebellum; 4, medulla oblongata. Fig. 593.—Frog without its cerebrum avoiding an object placed in its path. Fig. 594.—Frog without its cerebrum moving on an inclined board. Fig. 595.—Brain of pigeon seen from above. O, olfactory lobe; 1, cerebral hemispheres; 2, lateral part of the cerebellum; and 3, its central part or vermis; 4, medulla oblongata.

it sits. [If the flanks of such a frog be stroked, it croaks with the utmost regularity according to the number of times it is stroked. Langendorff has shown that a frog croaks under the same circumstances when both optic nerves are divided. It seems to be influenced by light, provided its optic lobes be uninjured; for, if an object be placed in front of it so as to throw a strong shadow, then on stimulating the frog it will spring not against the object, *a*, but in the direction, *b* (fig. 593), so that it seems to possess some kind of vision. Steiner finds that if a glass plate be substituted for an opaque object like a book, the frog always jumps against this obstacle. Its **balancing** movements on a board are quite remarkable and acrobatic in character. If it be placed on a board, and the board gently inclined (fig. 594), it does not fall off, as a frog with only its spinal cord will do, but as the board is inclined, so as to alter the animal's centre of gravity, it slowly crawls up the board until it reaches such a position that its equilibrium is restored. If the board be sloped as in fig. 594, it will crawl up until it sits on the edge, and if the board be still further tilted, the frog will move as indicated in the figure. It only does so, however, when the board is inclined, and it rests as soon as its centre of gravity is restored. It responds to every stimulus just like a complex machine, answering each stimulus with an appropriate action, and the movements come to an end when the stimulus ceases. It has been found, however, that if the frog be kept for a long time, in spite of the absence of regeneration of the cerebral hemispheres, there is a tendency for what may be apparently spontaneous movements to show themselves occasionally. But still apparently in such frogs there is wanting what is

ordinarily called "will." The frog without its cerebrum possesses all the nervous and other mechanisms required for the execution of many complex co-ordinated movements, but it seems to want the power of voluntarily originating impulses to set this machine in motion, *i.e.*, there is a want of spontaneity (*Goltz, Steiner*). Schrader, however, states that in a frog deprived of its cerebral hemispheres there is not a complete absence of spontaneity nor of ability to feed itself, and states that such frogs may bury themselves in the earth at the beginning of winter and in summer they may catch flies.]

A **pigeon** without its cerebral hemispheres (fig. 595) becomes drowsy, dull, and stupid, and behaves in a passive and motionless manner (fig. 596). When undisturbed it sits continuously, *as if in sleep*, but when stimulated, it exhibits complete harmony of all its movements; it can walk, fly, perch, and balance its body on one leg; there is no paralysis. [It regains its position if put on its side or back. When flying it can imperfectly avoid obstacles in its path.] The sensory nerves and those of special sensation conduct impulses to the remaining parts of the brain, but such impulses only discharge reflex movements, and they do not appear to excite conscious impressions. The bird starts when a pistol is fired close to its ear; it closes its eyes when it is brought near a flame, and the pupils contract; it turns away its head when the vapour of ammonia is applied to its nostrils. All these impressions are, perhaps, not perceived as conscious perceptions. The perceptive faculties—the will and memory—are abolished; the animal never takes food or drinks spontaneously. Food placed at the back part of its throat is swallowed [reflex act], or if its beak be plunged in corn it eats, and in this way the animal may be maintained alive for months (*Flourens*). [In a certain number of cases the drowsy condition diminishes or may even pass off, and the pigeon may exhibit what appear to be spontaneous movements, but still these movements are very different from those of an intact bird. These movements are not necessarily volitional. It never flies or feeds itself, although placed in the midst of plenty of food, but it may walk aimlessly about for a time, and then resume its usually stolid, sleepy attitude.]

Fig. 596.

Pigeon with its cerebral hemispheres removed.

Fish appear to behave differently. A carp with its cerebrum removed (fig. 609, VI. 1) can see and may even select its food, and seems to execute its movements voluntarily (*Steiner*, *Vulpian*).

[In Teleostean fishes, if the homologues of the cerebral ganglion be removed such fish appear at first sight like normal fish. They maintain their normal attitude, and swim by means of the tail and fins with precision, and in their course they avoid obstacles, as if still possessed of some sense of vision. In them also there is apparently not complete absence of spontaneity. They not only see, but they seek their food, and can discriminate between different kinds of food or objects thrown into the water. It seems, then, that such fish to some extent see, distinguish colours, catch prey, direct its movements, but it is more impulsive and less cautious than a normal fish. An Elasmobranch fish, such as the dog-fish, deprived of its cerebral ganglion, is quite unable to find its food, because removal of the cerebrum necessitates removal of the organ of smell by which this animal is guided to its food.]

Mammals, owing to the great loss of blood consequent on removal of the cerebrum, are not well suited for experiments of this kind. Immediately after the operation rabbits and rats show signs of great muscular weakness. When they recover, they present the same general phenomena as are observed in the pigeon.

When stimulated they run, as it were, blindfold against an obstacle. Vulpian heard a peculiar shriek or cry which such a rabbit makes under the circumstances. [They regain their equilibrium if placed on their side or back; they usually remain passive, taking no heed of food placed within their reach, but they masticate food placed in their mouth.] Sometimes even in man a peculiar cry is emitted in some cases of pressure or inflammation rendering the cerebral hemispheres inactive.

[The **dog** does not survive removal of the whole cerebrum at one time, but parts of the cerebral convolutions have been removed at different times. Animals, which survive the operation for a long time, can execute many complicated acts, the performance of their ordinary bodily movements being only somewhat interfered with, but they exhibit signs of spontaneity in their acts, which lead one to infer that they still possess some intelligence and volitional power. It is plain that the nervous machinery for executing most or all of the ordinary movements of the foregoing animals lies in some part of the nervous system other than the cerebral hemispheres—probably in the middle and hind brains].

[A study of the phenomena exhibited by animals deprived of their cerebral lobes goes to show that such animals not only maintain all their organic functions, but they still possess the power of equilibration, co-ordination of locomotion, some degree of emotional expression, and "adaptive reactions in accordance with impressions made upon their organs of sense" (*Ferrier*).]

Observations on **somnambulists** show that in man also complete harmony of all movements may be retained, without the assistance of the will or conscious impressions and perceptions. As a matter of fact, many of our ordinary movements are accomplished without our being conscious of them. They take place under the guidance of the basal ganglia.

The degree of intelligence in the animal kingdom is in relation to the size of the cerebral hemispheres, in proportion to the mass of the other parts of the central nervous system. Taking the brain alone into consideration, we observe that those animals have the highest intelligence in which the cerebral hemispheres greatly exceed the mid-brain in weight. The mid-brain is represented by the optic lobes in the lower vertebrates, and by the corpora quadrigemina in the higher vertebrates. In fig. 609, VI represents the brain of a carp; V, of a frog; and IV of a pigeon. In all these cases 1 indicates the cerebral hemispheres; 2, the optic lobes; 3, the cerebellum; and 4, the medulla oblongata. In the carp, the cerebral hemispheres are smaller than the optic lobes; in the frog, they exceed the latter in size. In the pigeon, the cerebrum begins to project backward over the cerebellum. The degree of intelligence increases in these animals in this proportion. In the dog's brain (fig. 609, II) the hemispheres completely cover the corpora quadrigemina, but the cerebellum still lies behind the cerebrum. In man the occipital lobes of the cerebrum completely overlap the cerebellum (fig. 606). [The projection of the occipital lobes over the cerebellum is due to the development of the frontal lobes pushing backwards the convolutions that lie behind them, and not entirely to increased development of the occipital lobes.]

Meynert's Theory.—According to Meynert, we may represent this relation in another way. As is known, fibres proceed downwards from the cerebral hemispheres, through the crusta or pes of the cerebral peduncle. These fibres are separated from the upper fibres or tegmentum of the peduncle by the locus niger, the tegmentum being connected with the corpora quadrigemina and the optic thalamus. The larger, therefore, the cerebral hemispheres, the more numerous will be the fibres proceeding from it. In fig. 564, II, is a transverse section of the posterior corpora quadrigemina, with the aqueduct of Sylvius and both cerebral peduncles of an adult man; *p*, *p*, is the crusta of each peduncle and above it lies the locus niger, *s*. Fig. 564, IV, shows the same parts in a monkey; III, in a dog; and V, in a guinea-pig. The crusta diminishes in the above series. There is a corresponding diminution of the cerebral hemispheres, and, at the same time, in the intelligence of the corresponding animals.

Sulci and Gyri.—The degree of intelligence also depends upon the number and depth of the convolutions. In the lowest vertebrates (fish, frog, bird) the furrows or sulci are absent (fig. 564, IV, V, VI); in the rabbit there are two shallow furrows on each side (III). The dog has a completely furrowed cerebrum (I, II). Most remarkable is the complexity of the sulci and convolutions of the cerebrum of the elephant, one of the most intelligent of animals. Nevertheless, some very stupid animals, as the ox, have very complex convolutions.

The absolute weight of the brain cannot be taken as a guide to the intelligence. The

elephant has *absolutely* the heaviest brain, but man has *relatively* the heaviest brain. [We ought also to take into account the complexity of the convolutions and the depth of the grey matter, its vascularity, and the number of connections between its nerve-cells.]

Time an Element in all Psychical Processes.—Every psychical process requires a certain time for its occurrence—a certain time always elapses between the application of the stimulus and the conscious reaction.

Nature of Stimulus.	Reaction Time.	Name of Observer.
Shock on left hand,	·12	Exner.
Shock on forehead,	·13	Do.
Shock on toe of left foot,	·17	Do.
Sudden noise,	·13	Do.
Visual impression of electric spark,	·15	Do.
Hearing a sound,	·16	Donders.
Current to tongue causing taste,	·16	v. Vintschgau and Hönigschmied.
Saline taste,	·15	Do.
Taste of sugar,	·16	Do.
,, acids,	·16	Do.
,, quinine,	·23	Do.

Reaction Time.—This time is known as "*reaction time*," and is distinctly longer than the simple reflex time required for a reflex act. It can be measured by causing the person experimented on to indicate by means of an electrical signal the moment when the stimulus is applied. The reaction time consists of the following events :—(1) The *duration of perception*, *i.e.*, when we become conscious of the impression ; (2) the duration of the time required to direct the *attention* to the impression, *i.e.*, the *duration of apperception ;* and (3) the *duration of the voluntary impulse*, together with (4) the time required for conducting the impulse in the afferent nerves to the centre, and (5) the time for the impulse to travel outwards in the motor nerves. If the signal be made with the hand, then the reaction time for the impression of *sound* is 0·136 to 0·167 second ; for taste, 0·15 to 0·23 ; touch, 0·133 to 0·201 second (*Horsch*, *v. Vintschgau and Hönigschmied*) ; for olfactory impressions, which, of course, depend upon many conditions (the phase of respiration, current of air), 0·2 to 0·5 second. Intense stimulation, increased attention, practice, expectation, and knowledge of the kind of stimulus to be applied, all diminish the time. Tactile impressions are most rapidly perceived when they are applied to the most sensitive parts (*v. Vintschgau*). The time is increased with very strong stimuli, and when objects difficult to be distinguished are applied (*v. Helmholtz and Baxt*). The time required to direct the **attention** to a number consisting of 1 to 3 figures, Tigerstedt and Bergquist found to be 0·015 to 0·035 second. Alcohol and the anæsthetics alter the time ; according to their degree of action, they shorten or lengthen it (*Kraplin*). In order that two shocks applied after each other be distinguished as two distinct impressions, a certain interval must elapse between the two shocks—for the ear, 0·002 to 0·0075 second ; for the eye, 0·044 to 0·47 second ; for the finger, 0·277 second.

[**The Dilemma.**—When a person is experimented on, and he is not told whether the right or left side is to be stimulated, or what coloured disc may be presented to the eye, then the time to respond correctly is longer.]

[**Drugs** and other conditions affect the reaction time. Ether and chloroform lengthen it, while alcohol does the same, but the person imagines he really reacts quicker. Noises also lengthen it.]

In **sleep and waking**, we observe the periodicity of the active and passive conditions of the brain. During sleep there is diminished excitability of the whole nervous system, which is only partly due to the fatigue of afferent nerves, but is largely due to the condition of the central nervous system. During sleep, we require to apply strong stimuli to produce reflex acts. In the deepest sleep the psychical or mental processes seem to be completely in abeyance, so that a person asleep might be compared to an animal with its cerebral hemispheres removed. Towards the approach of the period when a person is about to waken, psychical activity may manifest itself in the form of **dreams**, which differ, however from normal mental processes. They consist either of impressions, where there is no objective cause (hallucinations), or of voluntary impulses which are not executed, or trains of thought where the reasoning and judging powers are disturbed. Often, especially near the time of waking, the actual stimuli may so act as to give rise to impressions which become mixed with the thoughts of a dream. The diminished activity of the heart (§ 70, 3, *c*), the respiration (§ 126, 4), the gastric and intestinal movements (§ 213, 4), the formation of heat (§ 216, 4), and the secretions, point to a diminished excitability of the corresponding nerve-centres, and the diminished reflex excitability to a corresponding condition of the spinal cord. The pupils are contracted during sleep,

the deeper the latter is; so that in the deepest sleep they do not become contracted on the application of light. The pupils dilate when sensory or auditory stimuli are applied, and the lighter the sleep the more is this the case; they are widest at the moment of awaking (*Plotke*). [Hughlings Jackson finds that the retina is more anæmic than in the waking state.] During sleep, there seems to be a condition of increased action of certain sphincter muscles—those for contracting the pupil and closing the eyelids (*Rosenbach*). The soundness of the sleep may be determined by the intensity of the sound required to waken a person. Kohlschütter found that at first sleep deepens very quickly, then more slowly, and the maximum is reached after one hour (according to Mönninghoff and Priesenbergen after $1\frac{3}{4}$ hour); it then rapidly lightens, until several hours before waking it is very light. External or internal stimuli may suddenly diminish the depth of the sleep, but this may be followed again by deep sleep. The deeper the sleep the longer it lasts. [Durham asserts that the brain is anæmic, that the arteries and veins of the pia mater are contracted during sleep and the brain smaller; but is this cause or effect?]

The cause of sleep is the using up of the potential energy, especially in the central nervous system, which renders a restitution of energy necessary. Perhaps the accumulation of the decomposition-products of the nervous activity may also act as producers of sleep (? lactates—*Preyer*). Sleep cannot be kept up for above a certain time, nor can it be interrupted voluntarily. Many narcotics rapidly produce sleep. [The "diastolic phase of cerebral activity," as sleep has been called, is largely dependent on the absence of stimuli. We must suppose that there are two factors, one central, represented by the excitability of the cerebrum, which will vary under different conditions, and the other external, represented by the impulses reaching the cerebrum through the different sense-organs. We know that a tendency to sleep is favoured by removal of external stimuli, by shutting the eyes, retiring to a quiet place, &c. The external sensory impressions, indeed, influence the whole metabolism. Strumpell describes the case of a boy whose sensory inlets were all paralysed except one eye and one ear, and when these inlets were closed the boy fell asleep, showing how intimately the waking condition is bound up with sensory afferent impulses reaching the cerebral centres.]

[**Hypnotics**, such as opium, morphia, bromide of potassium, chloral, are drugs which induce sleep.]

Hypnotism, or Animal Magnetism.—[Most important observations on this subject were made by Braid of Manchester, whose results are confirmed by many of the recent re-discoveries of Weinhold, Heidenhain, and others.] Heidenhain assumes that the cause of this condition is due to an inhibition of the ganglionic cells of the cerebrum, produced by continuous feeble stimulation of the face (slightly stroking the skin or electrical applications), or of the optic nerve (as by gazing steadily at a small brilliant object), or of the auditory nerve (by uniform sounds); while sudden and strong stimulation of the same nerves, especially blowing upon the face, abolishes the condition. Berger attributes great importance [as did Carpenter and Braid long ago] to the psychological factor, whereby the attention was directed to a particular part of the body. The facility with which different persons become hypnotic varies very greatly. When the hypnotic condition has been produced a number of times, its subsequent occurrence is facilitated, *e.g.*, by merely pressing upon the brow, by placing the body passively in a certain position, or by stroking the skin. In some people the mere idea of the condition suffices. A hypnotised person is no longer able to open his eyelids when they are pressed together. This is followed by spasm of the apparatus for accommodation in the eye, the range of accommodation is diminished, and there may be deviation of the position of the eyeballs; then follow phenomena of stimulation of the sympathetic in the oblongata; dilatation of the fissure of the eyelids and the pupil, exophthalmos, and increase of the respiration and pulse. At a certain stage there may be a great increase in the sensitiveness of the functions of the sense-organs, and also of the muscular sensibility. Afterwards there may be analgesia of the part stroked, and loss of taste; the sense of temperature is lost less readily, and still later that of sight, of smell, and of hearing. Owing to the abolition or suspension of consciousness, stimuli applied to the sense-organs do not produce conscious impressions or perceptions. But stimuli applied to the sense-organs of a hypnotised person cause movements, which, however, are unconscious, although they stimulate voluntary acts. In persons with greatly increased reflex excitability, voluntary movements may excite reflex spasms; the person may be unable to co-ordinate his organs for speech.

Types.—According to Grützner, there are several forms of hypnotism:—(1) *Passive sleep*, where words are still understood, which occurs especially in girls; (2) owing to the increased reflex excitability of the striped muscles, certain *groups of muscles* may be contracted—a condition which may last for days, especially in strong people; at the same time ataxia may occur, and the muscles may fail to perform their functions (**artificial katalepsy**). During the stage of lethargy in hysterical persons, the tendon reflexes are often absent (*Charcot and Richer*); (3) *autonomy at call*, *i.e.*, the hypnotised person—in most cases the consciousness is still retained—obeys a command, in his condition of light sleep. When the hand is grasped or the head stroked, he executes involuntary movements—runs about, dances, rides on a stool, and the like; (4) *hallucinations* occur only in some individuals when they waken from a deep sleep, the hallucinations (usually consisting of the sensation of sparks of fire or odours) being very strong and well pronounced; (5) imitation is rare, ordinary movements, such as walking, are easily imitated,

the finer movements occur rarely. The "echo-speech" is produced by pressure upon the neck, speaking into the throat, or against the abdomen. Pressure over the right eyebrow often ushers in the speech. Colour-sensation is suspended by placing the warm hand on the eye, or by stroking the opposite side of the head (*Cohn*). Stroking the limbs in the reverse direction gradually removes the rigidity of the limbs and causes the person to waken. Blowing on a part does so at once. Insane persons can be hypnotised. Disagreeable results follow only when the condition is induced too often and too continuously.

Hypnotism in Animals.—A hen remains in a fixed position when an object is suddenly placed before its eyes, or when a straw is placed over its beak, or when the head of the animal is pressed on the ground and a chalk line made before its beak (Kircher's experimentum mirabile, 1644). [Langley has hypnotised a crocodile.] Birds, rabbits, and frogs remain passive for a time after they have been gently stroked on the back. Crayfish stand on their head and claws (*Czermak*).

375. STRUCTURE OF THE CEREBRUM—MOTOR CORTICAL CENTRES.

—[**Cerebral Convolution.**—A vertical section of a cerebral convolution consists of a thin layer of grey matter externally enclosing a white core or central white matter (figs. 597, 598). The cortex consists of cells and fibres embedded in a "molecular" matrix, and to some of the nerve-cells nerve-fibres proceed from the white matter. The nerve-cells of the cortex vary in size, form, and distribution in the different layers and also in different convolutions. [The layers of cells lie more or less parallel to the surface of the convolutions, so that the grey matter is thereby divided into a series of zones or layers. Usually five layers can be recognised. The thickness of the grey matter is about 3 mm., but it is 2 mm. in some parts of the occipital lobe, and 4·2 mm. in some parts of the ascending frontal convolution.] Taking such a convolution as the ascending frontal or **motor-area type**, we get the appearances shown in fig. 598. It is covered on its surface by the pia mater. (1) The most **superficial layer** is narrow, and consists of much neuroglia, a network of branched nerve-fibrils, which together form the chief mass of the abundant molecular ground-substance; a few scattered small multipolar nerve-cells, and a layer of very fine medullated nerve-fibres, which traverse it in a horizontal direction. The surface of the layer seems to consist of neuroglia alone. (2) **Layer of small pyramidal cells.** A layer (·25 mm. to ·75 mm. in thickness) of close-set, *small, angular* or *short pyramidal nerve-cells.* The cells are pyramidal and small, and give off processes which ramify and break up in the general molecular ground-substance of the cortex. It has not been proved that they possess median basilar axis-cylinder processes. (3) **Layer of large pyramidal cells.** The thickest layer (·4 mm. to ·1 mm.) or "formation of the cornu ammonis," consists of many layers of *large pyramidal cells*, which are larger in the deeper than in the more superficial layers. They are not so closely packed together, as many granules lie between them. At the lowest part of this layer the cells are larger than elsewhere, presenting some resemblance to the cells of the anterior cornu of the grey matter of the spinal cord. By some it is described as a special layer and termed the *ganglion-cell layer*. This layer is specially well marked in those convolutions which are described as containing motor centres, but pyramidal cells resembling these are found over the whole cortex. The cells are connected by their axial-cylinder process to white nerve-fibres. Amongst the large cells are a few small angular-looking cells, which become more numerous lower down. (4) The **fourth layer**—a narrow layer (·35 mm. to ·15 mm.) is composed of numerous small, branched, irregular, ganglionic cells—the "*granular formation*" of Meynert. In the motor areas mixed with these are large pyramidal cells, disposed in groups, called "cell-clusters." This layer is divided like the succeeding one into vertical columns by the groups of white fibres which pass outwards into the cortex from the central white matter. There are also horizontal fine medullated fibres in it.

(5) The **fifth layer** next the central white matter (·1 mm. thick), and from which it is not everywhere sharply defined, contains scattered in it spindle-shaped *fusiform* branched cells—the *claustral formation* of Meynert—lying for the most

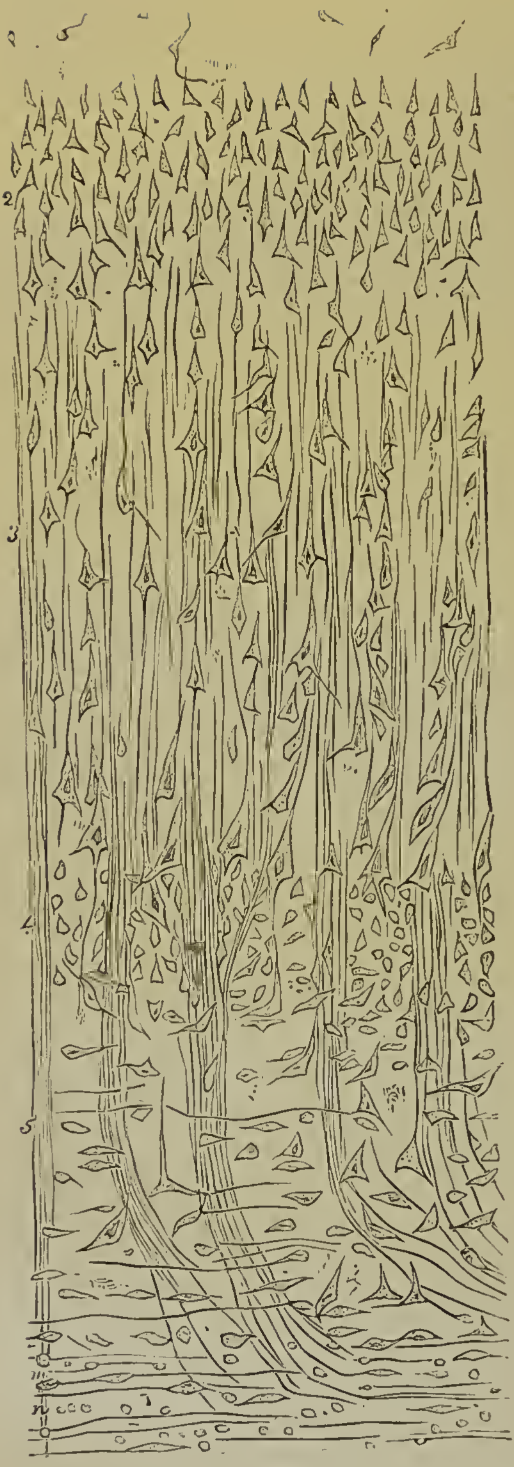


Fig. 597.

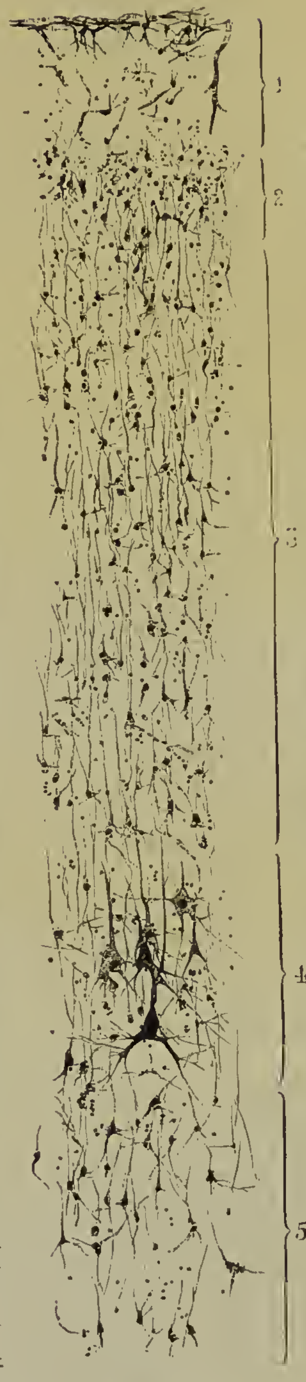


Fig. 598.

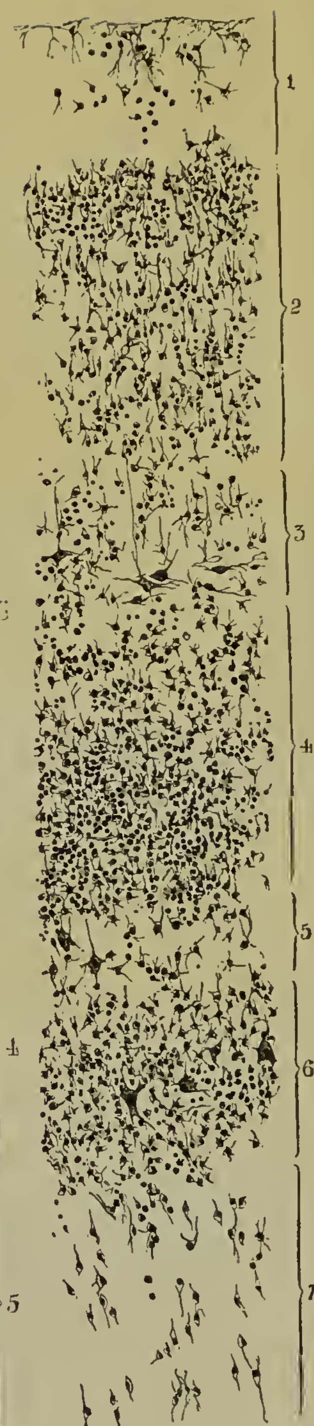


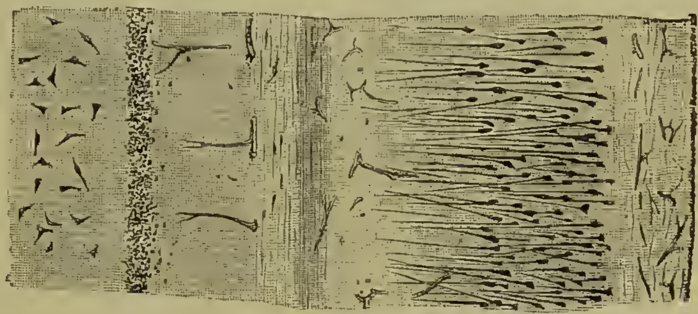
Fig. 599.

Fig. 597.—Vertical section of a motor cerebral convolution of man. 1, superficial layer; 2, layer of small, and 3, of large pyramidal cells; 4, granule formation; 5, claustral formation; *m*, medulla. Fig. 598.—Cortex of motor area of brain of monkey (×150). 1, superficial layer; 2, small angular cells; 3, pyramidal cells; 4, ganglionic cells and cell-clusters; 5, fusiform cells (*Ferrier*, after *Bevan Lewis*). Fig. 599.—Cortex of occipital lobe. 1, superficial layer; 2, small angular cells; 3, 5, pyramidal cells; 4, granule layer; 6, granules and ganglionic layer; 7, spindle-cells (*Ferrier*, after *Bevan Lewis*).

part parallel to the surface of the convolution. It is broken up into vertical columns by the white fibres proceeding from the central white matter into the cortex. Then follows the **central white matter** (m), consisting of medullated nerve-fibres, which run in groups into the grey matter, where they lose their myelin. The fibres are somewhat smaller than in the other parts of the nervous system (diameter $\frac{1}{1000}$ inch), and between them lie a few nuclear elements.

It will be seen that no layer is composed exclusively of one form of cell. In the above, which represents the **motor type**, such as occurs in the "motor areas" of the brain, the layer is very thick, the pyramidal cells which it contains are both large and numerous, and in the fourth layer there are very large pyramidal cells (110 μ to 50 μ), which are largest at the upper part of the ascending frontal convolution.]

[In the **sensory type**, as in the **occipital lobe** (fig. 599), the first and second layers are not unlike the corresponding layers in the motor type, and the fusiform cells in the seventh layer also resemble the latter. The layer of pyramidal cells (3) is not so large, while its deeper part, sometimes called the "ganglion-cell layer," contains no large cells. (5) Between the two is (4), a layer with numerous angular granule-like bodies or cells, the "granule-layer." The abundance of these small "nuclear" with "angular" cells is the chief characteristic of the occipital region. There are also numerous horizontal medullated fibres in the fourth layer.]



Fd Fig. 600. C. Am.

Cortex of the cornu ammonis (C. Am.), and a part of the Fascia dentata (*Fd*). *Vli.*, inferior horn of the lateral ventricle. × 20.

[The **hippocampus** or **cornu ammonis**, a portion of the cerebral cortex peculiarly modified, and in part projecting into the descending horn of the lateral ventricle, contains, besides a layer of neuroglia and some white matter on the surface, a regular series of pyramidal cells of the third layer, which give it a characteristic appearance. This is the part which varies most. The fourth and fifth layers are small, while the pyramidal cells of the third layer are remarkably long (fig. 600).

[In the **frontal** non-motor region the third layer is much thinner than in the motor areas, while the layer of fusiform cells is well developed.]

[It is to be remembered that the transition from one type to the other takes place gradually and that the transition from one anatomical region to another is very gradual.]

[**Pyramidal Cells of the Cortex.**—Each cell is more or less pyramidal in shape, granular or fibrillated in appearance and with a large conspicuous nucleus. Each cell gives off several processes—(a) an **apical process**, which is often very long, and runs towards the surface of the cerebrum, and as it does so gives off lateral processes, which break up into fine fibrils. (b) The unbranched axial cylinder, **median basilar process**, which is an axial cylinder process, and becomes continuous with the axial cylinder of a nerve-fibre of the white matter. It ultimately becomes invested by myelin. Sometimes the axis-cylinder process divides at a node of Ranvier, like the T-shaped fibres of the spinal ganglion. (c) The **lateral processes** are given off chiefly near the base of the cell, and they soon branch to form part of the ground plexus or molecular ground-substance of fibrils which everywhere pervades the grey

matter. The largest pyramidal cells—those known as giant cells—in the motor areas may be 110–50 μ, but the ordinary large pyramidal cells are 20 to 40 μ, and

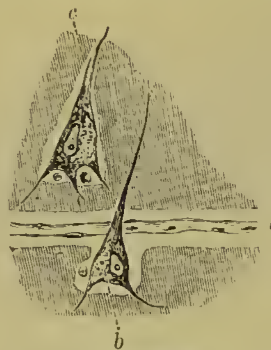


Fig. 601.

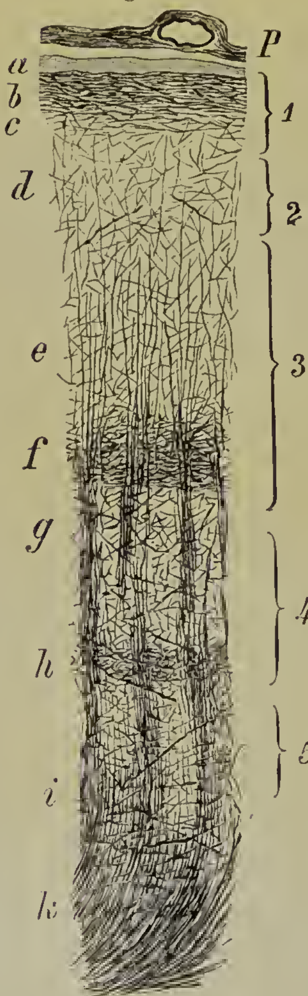


Fig. 602.

Fig. 603.

Fig. 601.—Perivascular and pericellular lymph-spaces. a, capillary with a lymph-space communicating with the pericellular lymph-space b, round the cell a lymph-space c, containing two lymph-corpuscles. $\times 150$. Fig. 602.—Vertical section of a frontal convolution (Weigert's method) $\times 50$. P, pia mater; 1–5, five layers of Meynert; a, superficial layer of connective-tissue; b–i, successive layers of medullated nerve-fibres; k, white matter. Fig. 603.—Section of a cerebral convolution stained by Golgi's method. 1, neuroglia layer; 2, layer of small cells; 3, layer of large pyramidal cells; 4, layer of irregular cells.

the small pyramidal cells (which have not been proved to possess an axial cylinder process) are 8–12 μ in breadth. The large pyramidal cells are trophic in function for the very long nerve-fibres which are connected with them.]

[**Golgi's method of staining nerve-cells.**—The nerve-cells are stained black by long immersion in silver nitrate or mercuric chloride solution after the brain is hardened in a chromium salt. The metal is deposited in, or rather on, the cell and its processes, and in this way the ramifications of these cells can be traced for a long distance.]

Each cell is surrounded by a **lymph-space** in which it lies. The blood-vessels are provided with a perivascular space, which communicates with the pericellular lymph-space, as in fig. 601.

[**Nerve-fibres in the Cortex.**—The ordinary methods of hardening the brain do not enable us to detect the enormous number of **medullated nerve-fibres** in the grey matter. By using Exner's osmic acid method, or Weigert's or Pal's method, we obtain such a result as is shown in fig. 602. Under the pia (P) is a layer of connective-tissue (*a*) devoid of nerve-fibres. Beneath it is a layer (*b*) occupying about the half of the outer layer, which is almost entirely taken up by medullated nerve-fibres ; most of these are fine, but a few of them are coarse, and run parallel to the surface and tangential to the arc of the outer contour of the convolution. Internal to this is a layer of medullated fibres (*c*), which cross each other in various directions ; while a similar network (*d*) occur in the small-celled layer. (2) In the layer of large pyramidal cells (3) there are bundles of medullated fibres, running radially (*e*) ; but at the lower part of this layer there is a very dense network (*f*), forming (in a Weigert's preparation) a dense, dark band, corresponding to the outer layer of Baillarger. In the layers marked (*g* and *h*), which are partly in the third and partly in the fourth cortical layer, the radial arrangement is more marked and more compact, and the thick fibres are more numerous. In the middle is (*h*) a narrow dense network corresponding to Baillarger's inner layer. The lower part of the fourth layer, and the whole of the fifth, are occupied by *i*. It is to be remembered that all the convolutions do not present exactly the same structure and arrangement (*Obersteiner*).]

[The existence of such an enormous number of nerve-fibres passing from the central white matter into the cortex makes it evident that the white matter must be connected to the grey cortical matter by some means other than axis-cylinder processes, the prolongations of the median basilar processes of the pyramidal cells. Perhaps most of the white fibres entering the cortex, either as callosal, pyramidal, tegmental, or association fibres split up into fibrils to form a large part of the molecular ground-substance. We do not know if they become continuous anatomically with the fibrils.]

[**Variations.**—The grey matter differs in different parts of the brain. In the grey matter of the cornu ammonis, the large pyramidal cells of (3) make up the chief mass (fig. 600) ; in the claustrum (4) is most abundant. In the **central convolutions** (ascending frontal and parietal), according to Betz, Mierzejewski, and Bevan Lewis, very large pyramidal cells are found in the lower part of the third layer. Similar cells have been found in the posterior extremities of the frontal convolutions in some animals—the posterior parietal lobule, and para-central lobule, all of which have motor functions. In those convolutions, which are regarded as subserving **sensory** functions, a somewhat different type prevails, *e.g.*, the occipital gyri or annectant convolution (*B. Lewis*). The very large pyramidal cells are absent, while the granule layer exists as a well-marked layer between the layer of large pyramidal cells and the ganglion cell-layer (fig. 599).]

[Fuchs finds that there are no medullated fibres either in the cortex or medulla until the end of the first month of life. The medullated fibres appear in the uppermost layer at the fifth month, and in the second at the end of the first year, the radial bundles in the deeper layers at the second month. The medullated fibres increase until the seventh or eighth year, when they have the same arrangement as in the adult.]

[**Results of Golgi's Method.**—Fig. 603 shows a general view of the nerve-cells of the cortex cerebri stained by Golgi's method. The pyramidal cells give off branched protoplasmic processes and a central axial cylinder process which becomes continuous with a medullated nerve-fibre in the white matter (figs. 603, 604).]

[**Blood-Vessels.**—The adventitia of the small cerebral vessels contains pigment and granular cells, filled with oil-granules. In the new-born child, the blood-vessels of the brain are beset with cells, filled with fatty granules. Perhaps the granules supply part of the material for the formation of the myelin sheath on the nerve-fibres. About the fifth year the fat is replaced by a yellow pigment. In adults, yellow or brown glancing pigment-granules are found in the adventitia of the arteries. In the adventitia of the veins there is no pigment, but generally

some fat. The grey matter is much more vascular than the white, and when injected, a section of a convolution presents the appearance shown in fig. 605. The **nutritive** arteries consist of—(*a*) the long **medullary arteries** (1) which pass from the pia mater through the grey matter into the central white matter or centrum ovale. They are **terminal** arteries, and do not communicate with each other in their course; thus, they supply independent vascular areas; nor do they anastomose with any of the arteries derived from the ganglionic system of blood-vessels; 12 to 15 of them are seen in a section of a convolution. (*b*) The short **cortical nutritive** arteries (2) are smaller and shorter than the foregoing. Although some of them enter the white matter, they chiefly supply the cortex, where they form an open meshed plexus in the first layer (*a*), while in the next layer (*b*) the plexus of capillaries is dense, the plexus again being wider in the inner layers (*c*).]

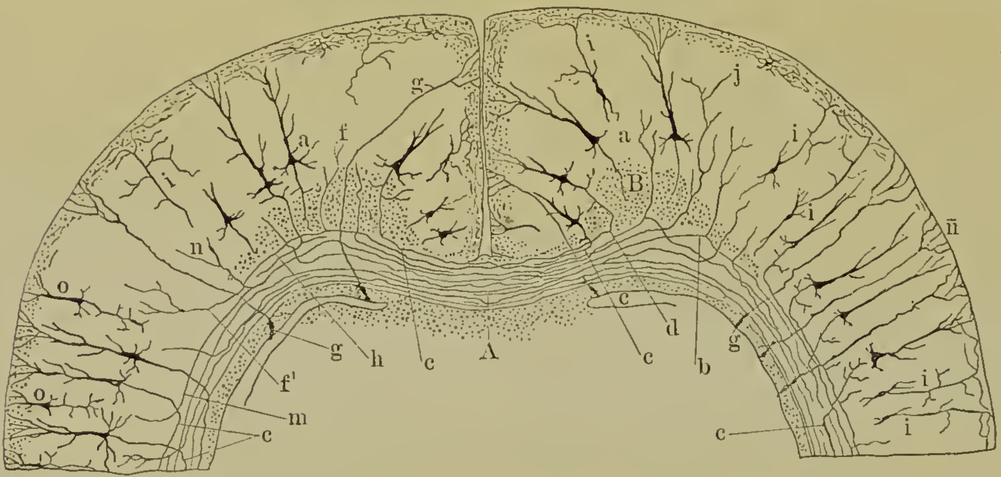


Fig. 604.

Scheme of a tranverse section of the cerebrum of a new-born rat by Golgi's method (*Cayal*). A, corpus callosum; B, antero-posterior fibres arising from the large pyramidal cells; C, lateral ventricle; *a*, large pyramidal cell whose axis-cylinder process passes into the anterior posterior layer; *b*, fibre of the corpus callosum bifurcating; *c*, callosal fibre; *d*, callosal fibre arising from a pyramidal cell; *e*, axis-cylinder process descending obliquely to enter the corpus callosum; *f*, final ramifications of a callosal fibre in the grey matter of the cortex; *h*, collateral fibre from a large pyramidal cell; *g*, epithelial cell ramifying in the surface of the cortex cerebri, *n*; *i*, fusiform cells with the axis-cylinder process ascending to the molecular layer; *j*, final ramification of a callosal fibre arising in the opposite side of the cortex.

[**Central** or **Ganglionic Arteries.**—From the trunks constituting the circle of Willis (fig. in § 381), branches are given off, which pass upwards and enter the brain to supply the basal ganglia with blood. They are arranged in several groups, but they are all **terminal**, each one supplying its own area, nor do they anastomose with the arteries of the cortex.]

Cerebral Arteries.—From a practical point of view, the distribution of the blood-vessels of the brain is important. The artery of the Sylvian fissure supplies the *motor* areas of the brain in animals; in man, the præcentral lobule is supplied by a branch of the anterior cerebral artery (*Duret*). The region of the third left frontal convolution, which is connected with the function of speech, is supplied by a special branch of the Sylvian artery. Those areas of the frontal lobes whose injury results in disturbance of the intelligence, are supplied by the anterior cerebral artery. Those regions of the cortex cerebri, whose injury, according to Ferrier, causes hemianæsthesia, are supplied by the posterior cerebral artery.

[In connection with the localisation of the centres in the cortex, it is important to be thoroughly acquainted with the arrangement of the **cerebral convolutions**. Each half of the outer cerebral

surface is divided by certain fissures into five lobes—**frontal, parietal, occipital, temporo-sphenoidal,** and **central,** or **island of Reil.** The **frontal lobe** (fig. 606) consists of three convolutions, with numerous secondary folds running nearly horizontal, named superior (F_1), middle (F_2), and inferior (F_3) frontal convolutions. Behind these is a large convolution, the ascending frontal (A), which ascends almost vertically, immediately behind these—separated from them, however, by the præcentral fissure (f_3), and mapped off behind by the fissure of Rolando, or the central sulcus (*c*).]

[The **parietal lobe** (fig. 606, P) is limited in front by the fissure of Rolando, below in part by the Sylvian fissure and behind by the parieto-occipital fissure. It consists of the ascending parietal (posterior central) convolution (fig. 606, B), which ascends just behind the fissure of Rolando, and parallel to the ascending frontal, with which it is continuous below; above, it becomes continuous with the superior parietal lobule (P_1), while the latter is separated from the inferior parietal lobule ("*pli courbe*") by the interparietal sulcus. The inferior parietal lobule consists of (*a*) a part arching over the upper end of the Sylvian fissure, the supramarginal convolution (P_2), which is continuous with the superior temporo-sphenoidal convolution. Behind is (*b*) the angular gyrus (P_2'), which arches round the posterior end of the parallel fissure, and becomes connected with the middle temporo-sphenoidal convolution.]

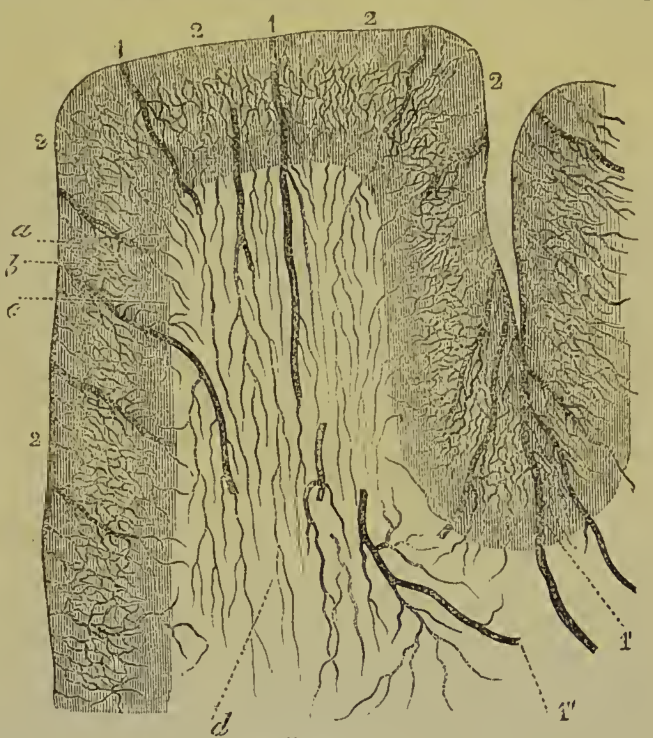


Fig. 605.

1, 1, medullary arteries; and 1', 1', in groups between the convolutions; 2, 2, arteries of the cortex cerebri; *a*, large meshed plexus in first layer; *b*, closer plexus in middle layer; *c*, opener plexus in the grey matter next the white substance, with its vessels (*d*).

[The **temporo-sphenoidal** or **temporal lobe** (fig. 606, T) consists of three horizontal convolutions — superior, middle, and inferior—the two former being separated by the parallel sulcus, while the whole lobe is mapped off from the frontal by the Sylvian fissure (S).]

[The **occipital lobe** (fig. 606, O) is small, forms the rounded posterior end of the cerebrum, and is separated from the parietal lobe by the parieto-occipital fissure, which fissure is bridged over at the lower part by the four annectant gyri (*plis de passage* of Gratiolet). It has three convolutions—superior (O_1), middle (O_2), and inferior (O_3)—on its outer surface.]

[The **central lobe** or **island of Reil**, consists of five or six short, straight convolutions (gyri operti) radiating outwards and backwards from near the anterior perforated spot, and can only be seen when the margins of the Sylvian fissure are pulled asunder. The **operculum**, consisting of the extremities of the inferior frontal, ascending parietal, and frontal convolutions, lie outside it, cover it, and conceal it from view.]

[On the **inner** or **mesial** surface of the cerebrum are—the **gyrus fornicatus** (fig. 607, Gf), or convolution of the corpus callosum, which runs parallel to and bends round the anterior and posterior extremities of the corpus callosum, terminating posteriorly in the gyrus uncinatus or gyrus hippocampi (fig. 607, H), and ending anteriorly in a crooked extremity, the subiculum cornu ammonis (fig. 607, U). Above it is the calloso-marginal fissure (fig. 607, *cm*), and running parallel to it is the **marginal convolution** (fig. 607), which lies between the latter fissure and the margin of the longitudinal fissure; it is, however, merely the mesial aspect of the frontal and parietal convolutions. The **quadrate lobule** or **præcuneus** lies (fig. 607, Pi) between the posterior extremity of the calloso-marginal fissure and the parieto-occipital fissure; it is merely the mesial aspect of the ascending parietal convolution. The parieto-occipital fissure terminates below in the **calcarine fissure** (fig. 607, *oc*), and the latter runs backwards in the occipital lobe dividing it into two branches, *oc'*, *oc''*. Between the parieto-occipital and calcarine fissures lies the wedge-shaped lobule termed the **cuneus** (fig. 607, Oz). The calcarine fissure indicates on the surface the position of the *calcar avis* or **hippocampus minor**, in the posterior cornu of the lateral ventricle. The **dentate fissure** or *sulcus hippocampi* (fig. 480, *h*)

marks the position of the elevation of the hippocampus major, or cornu ammonis, in the lateral ventricle. The **temporo-sphenoidal lobe** terminates anteriorly in the **uncinate gyrus**, while, running along the former and the occipital lobes, is the **collateral fissure** (occipito-temporal sulcus), which marks the position of the eminentia collateralis in the descending cornu of the lateral ventricle, while it also separates the *superior* from the *inferior* temporo-occipital convolutions (T_4 and T_5).]

[**Transverse or Commissural Fibres.**—The **corpus callosum** unites the two cerebral hemispheres. Fibres originate from all parts of the cerebral cortex (but only to a small extent from the temporal convolutions), and converge to the thick flattened arched band of the corpus callosum, intercrossing in the white matter of the cerebrum with the fibres of the corona radiata,

Fig. 606.

Left side of the human brain (diagrammatic). F, frontal; P, parietal; O, occipital; T, temporo-sphenoidal lobe; S, fissure of Sylvius; S′, horizontal, S″, ascending ramus of S; c, sulcus centralis, or fissure of Rolando; A, ascending frontal, and B, ascending parietal convolution; F_1, superior, F_2, middle, and F_3, inferior frontal convolutions; f_1, superior, and f_2, inferior frontal fissures; f_3, sulcus præcentralis; P, superior parietal lobule; P_2, inferior parietal lobule, consisting of P_2, supra-marginal gyrus, and P_2', angular gyrus; *ip*, sulcus interparietalis; *cm*, termination of calloso-marginal fissure; O_1, first, O_2, second, O_3, third occipital convolutions; *po*, parietal-occipital fissure; *o*, transverse occipital fissure; o_2, inferior longitudinal occipital fissure; T_1, first, T_2, second, T_3, third temporo-sphenoidal convolutions; t_1, first, t_2, second temporo-sphenoidal fissures.

i.e., the fibres of the crusta and tegmentum, ascending to the cortex cerebri. They are supposed to connect corresponding convolutions in opposite hemispheres.]

[The **anterior white commissure** at the front of the third ventricle connects the temporo-sphenoidal lobes of opposite sides. It proceeds from one side through the inner and middle divisions of the lenticular nucleus to the opposite side of the brain. A very small part belongs to the olfactory tract.]

[The **middle or soft commissure** of the third ventricle is really a part of the central grey matter.]

[The **posterior commissure** connects chiefly the two optic thalami, and perhaps also the tegmentum on the two sides.]

Association fibres pass from one convolution to another on the same hemisphere.

Longitudinal Commissure.—The fornix begins in grey matter of the corpora albicantia, while as it arches backwards its posterior pillars diverge and pass in the walls of the descending horn of the lateral ventricle.

Motor Areas or Regions.—In 1870 Fritsch and Hitzig discovered a series of circumscribed regions on the surface of the cerebral convolutions of the dog, whose

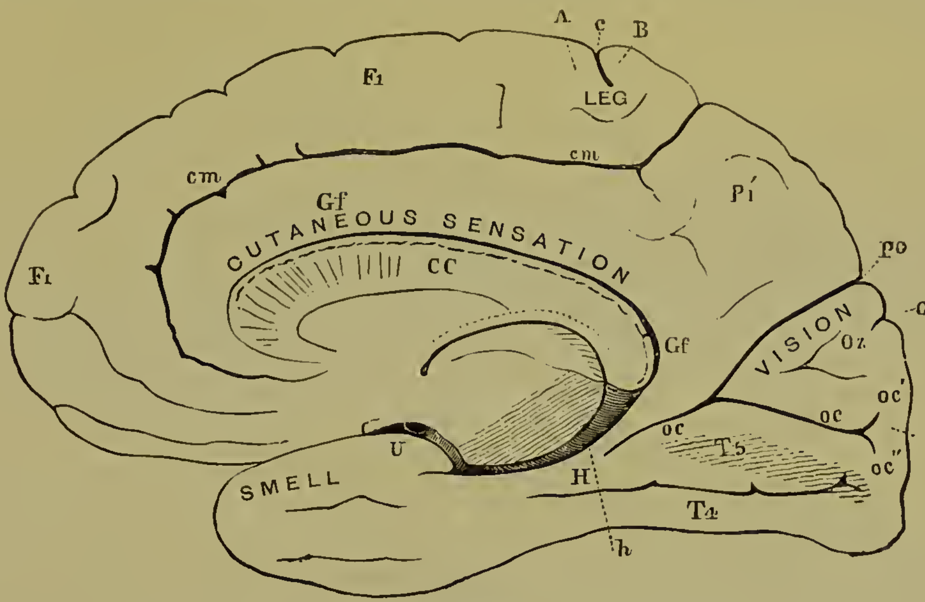


Fig. 607.

Median aspect of the right hemisphere. CC, corpus callosum divided longitudinally; Gf, gyrus fornicatus; H, gyrus hippocampi; *h*, sulcus hippocampi; U, uncinate gyrus; *cm*, calloso-marginal fissure; F, first frontal convolution; *c*, terminal portion of fissure of Rolando; A, ascending frontal; B, ascending parietal convolution and paracentral lobule; P_1', præcuneus or quadrate lobule; Oz, cuneus; Po, parieto-occipital fissure; o_1, transverse occipital fissure; *oc*, calcarine fissure; *oc'*, superior, *oc''*, inferior ramus of the same; D, gyrus descendens; T_4, gyrus occipito-temporalis lateralis (lobulus fusiformis); T_5, gyrus occipito-temporalis medialis (lobulus lingualis).

stimulation by means of electricity causes co-ordinated *movements* in quite distinct groups of skeletal muscles of the *opposite* side of the body (fig. 609, I, II) [while stimulation of some adjacent areas are not followed by any such movements].

Methods—Stimulation.—The surface of the cerebrum is exposed in an animal (dog, monkey) by removing a part of the skull covering the so-called motor convolutions and dividing the dura mater. When the convolutions are fully exposed, a pair of blunt non-polarisable (§ 328) needle electrodes are applied near each other to various parts of the cerebral surface. We may employ the closing or opening shock of a **constant current**, or the constant current may be rapidly interrupted, the current being of such a strength as to be distinctly perceived when it is applied to the tip of the tongue (*Fritsch and Hitzig*). Or, the **induced current** may be used, also of such a strength that it is readily felt when applied to the tip of the tongue (*Ferrier*, 1873). The cerebrum is completely *insensible to severe operations made upon it.*

The areas of the cerebral cortex, whose stimulation discharges the characteristic movements, are regarded by some as *actual centres*, because the reaction-time after stimulation of the centres and the duration of the muscular contraction are longer than when the subcortical fibres which lead towards the deeper parts of the brain are stimulated. Another circumstance favouring this view is that the excitability of these areas is influenced by the stimulation of afferent nerves (*Bubnoff and Heidenhain*). It may be that these centres are acted upon by voluntary impulses in the execution of voluntary movements. Hence, they have been called "*psychomotor centres.*" [At any rate, these areas have a definite relation to certain motor acts,

and perhaps it is well to speak of them as "areas of representation" of the function to which they are related.] The motor areas of the cerebrum (dog, cat, sheep) are characterised by the presence of specially large pyramidal cells (*Betz, Merzejewsky, Bevan Lewis*); while similar cells were found by Obersteiner in the areas marked 4 and 8 (fig. 609), and Betz found them in the ascending frontal convolution of man, in the third frontal convolution, and in the island of Reil. O. Soltmann found that stimulation of the motor areas in **newly-born** animals is without result, while only the deeper fibres of the corona radiata are excitable.

Modifying Conditions.—In the condition of *deep* narcosis produced by chloroform, ether, chloral, morphia, or in apnœa, the excitability of the centres is abolished (*Schiff*), whilst the subcortical conducting paths still retain their excitability (*Bubnoff and Heidenhain*). Small doses of these poisons and also of atropin at first increase the excitability of the centres. Moderate loss of blood excites them, while a great loss of blood diminishes and then abolishes the excitability (*Munk and Orschansky*). Slight inflammation increases, while cooling diminishes, the excitability. If the cortex cerebri be removed in animals, the excitability of the fibres of the corona radiata is completely abolished about the fourth day, just as in the case of a peripheral nerve separated from its centre (*Albertoni, Dupuy, Franck and Pitres*).

Stimulation of Subcortical Parts.—As the fibres of the corona radiata converge towards the centre of the hemisphere, it is evident that, after removal of the cortex, stimulation of these fibres in the deeper parts of the hemisphere is followed by the same motor effects (*Gliky and Eckhard*). The stimulus is applied merely to a deeper part of the motor path. If the stimulus be applied to parts situated still more deeply, as for example to the *internal capsule*, general contraction of the muscles on the opposite side is the result.

Time Relations of the Stimulation.—According to Franck and Pitres, the time which elapses between the moment of stimulation of the cortex and the resulting movement, after deducting the period of latent stimulation for the muscles, and the time necessary for the conduction of the impulse through the cord and nerves of the extremities, is 0·045 second. Heidenhain and Bubnoff found that, during moderate morphia narcosis, when the stimulating current was increased in strength, the muscular contraction and the reaction-time became shorter. After removal of the cortex, the occurrence of the muscular contraction from the moment of stimulation of the white matter is diminished $\frac{1}{4}$ to $\frac{1}{3}$. The form of the muscular contraction is longer and more extended when the cortex, than when the subcortical paths, are stimulated. If the animal (dog) be in a state of high reflex excitability, these differences disappear; in both cases the contraction follows very rapidly (*Bubnoff and Heidenhain*). If the stimulus be very strong the muscles of the *same* side may contract, but somewhat *later* than those of the opposite side. If the motor areas for the fore and hind limbs be stimulated simultaneously, the latter contract somewhat after the former.

Number of Stimuli.—If 40 stimuli per second be applied to a motor area, then the corresponding muscles yield 40 single contractions; while with 46 single stimuli per second there results a continued complete contraction (*Franck and Pitres*). In one and the same animal, the *same number of stimuli* is required to produce a continuous contraction, whether the cortical centre, the motor nerve, or even the muscle itself be stimulated. With very feeble stimuli, **summation of stimuli** takes place, for the muscular contraction only begins after several ineffective stimuli have been applied. [It is generally held that the rhythm of a contracting muscle is the same as the rhythm of the stimuli applied to its motor nerve, but Schäfer and Horsley contend that this holds good for rates of stimuli to about 10 or 12 per second. They find that the same is true for the cortex cerebri, corona radiata, and medulla spinalis, viz., that the muscular response does not vary with the rhythm, *i.e.*, number of stimuli per sec.), but that the rhythm is constant—about 10 per sec.—and independent of the number of stimuli per sec., provided they are above 10 per sec. applied to these parts. Indeed, all voluntary contractions show a similar rate of undulation in the muscle-curve. Perhaps the rhythm of the efferent impulses is modified in the motor nerve-cells of the spinal cord.]

[The matter, as regards electrical stimulation of the cortex cerebri, resolves itself into this, that stimulation of certain cortical areas always causes contraction in definite muscles or groups of muscles, resulting, as a rule, in definite co-ordinated movements on the *opposite* side of the body; the areas have been called "**motor areas.**" In some cases, however, stimulation of an area on one side results in bilateral movements in the case of corresponding muscles on opposite sides of the body, that usually act together, *e.g.*, those of the eyes and trunk. They have been

mapped out and ascertained in a large number of animals, and the question comes to be—Are there similar areas in man?]

Primary Fissures and Convolutions of the Dog's Brain.—The position of the motor centres in the dog's brain is indicated in fig. 609, I, and II. The dog's brain is marked by two "primary fissures," viz., the **sulcus cruciatus** (S.), which intersects the longitudinal fissure at a right angle at the junction of its anterior with its middle third. This fissure has been called

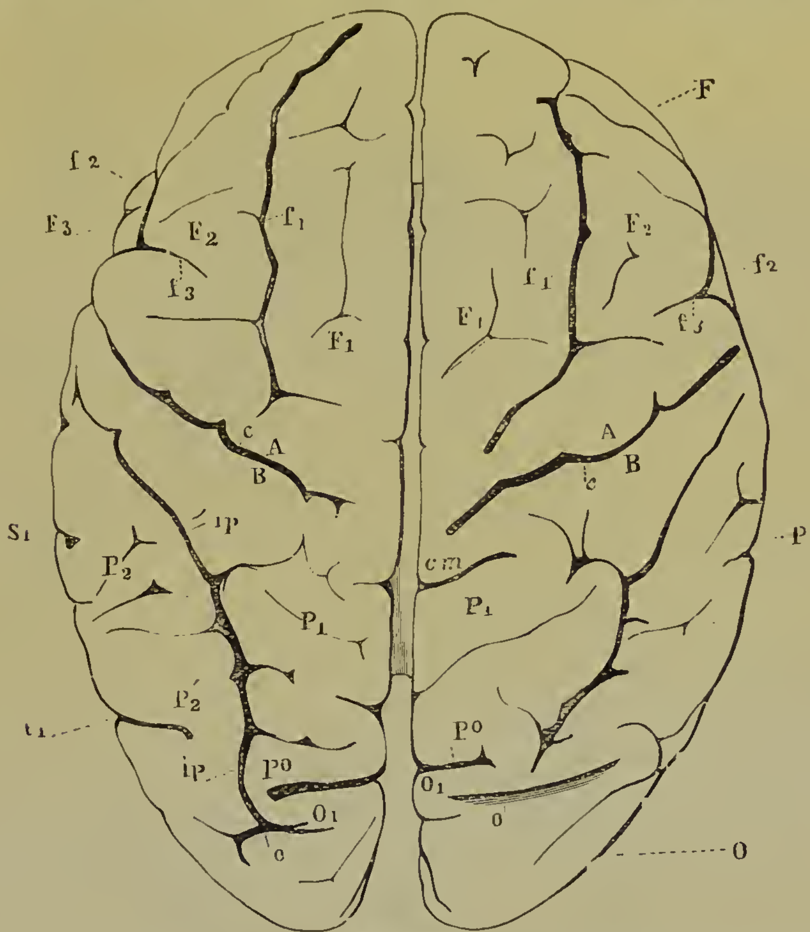


Fig. 608.

View of the brain from above (semi-diagrammatic). S_1, end of ramus of the Sylvian fissure. The other letters refer to the same parts as in fig. 606.

the sulcus frontalis, or the fissura coronalis. [It is bounded in front and behind by the "**sigmoid gyrus.**"] The second primary fissure is the **fossa Sylvii** (F). Four "**primary convolutions,**" in addition, are arranged with reference to these primary fissures. The first primary convolution (I), in the form of a sharply curved knee, embraces the fossa Sylvii (F). The second convolution (II) runs nearly parallel to the first. The fourth primary convolution (IV) bounds the longitudinal fissure, and is separated from its fellow of the opposite side by the falx cerebri; anteriorly it embraces the sulcus cruciatus (S), so that it is divided into two parts by this sulcus, a part, the gyrus præcruciatus or præfrontalis, lying in front of the sulcus, and the gyrus postcruciatus (postfrontalis) lying behind it. The third primary convolution (III) runs parallel to the fourth. Some authors count the convolutions from the longitudinal fissure outwards. In fig. 609, I and II, the **motor areas** or *centres* are indicated by dots on the individual primary convolutions. We must remember, however, that the centres are not mere points, but that they vary in size from that of a pea upwards, according to the size of the animal. Motor areas have been mapped out in the brain of the monkey, rabbit, rat, bird, and frog.

Position of the Motor Centres (Dog).—Fritsch and Hitzig, in 1870, mapped out the following motor areas, whose position may be readily found on referring to fig. 609:—1, is the centre for the *muscles of the neck*; 2, for the extensors and adductors of the *fore limb*; 3, for the flexion and rotation of the fore leg; 4, for the movements of the *hind limb*, which Luciani and Tamburini resolved into two antagonistic centres; 5, for the *muscles of the face*, or the facial

centre. In 1873 Ferrier discovered the following additional centres :—6, for the lateral switching movements of the *tail;* 7, for the retraction and abduction of the fore limb ; 8, for the

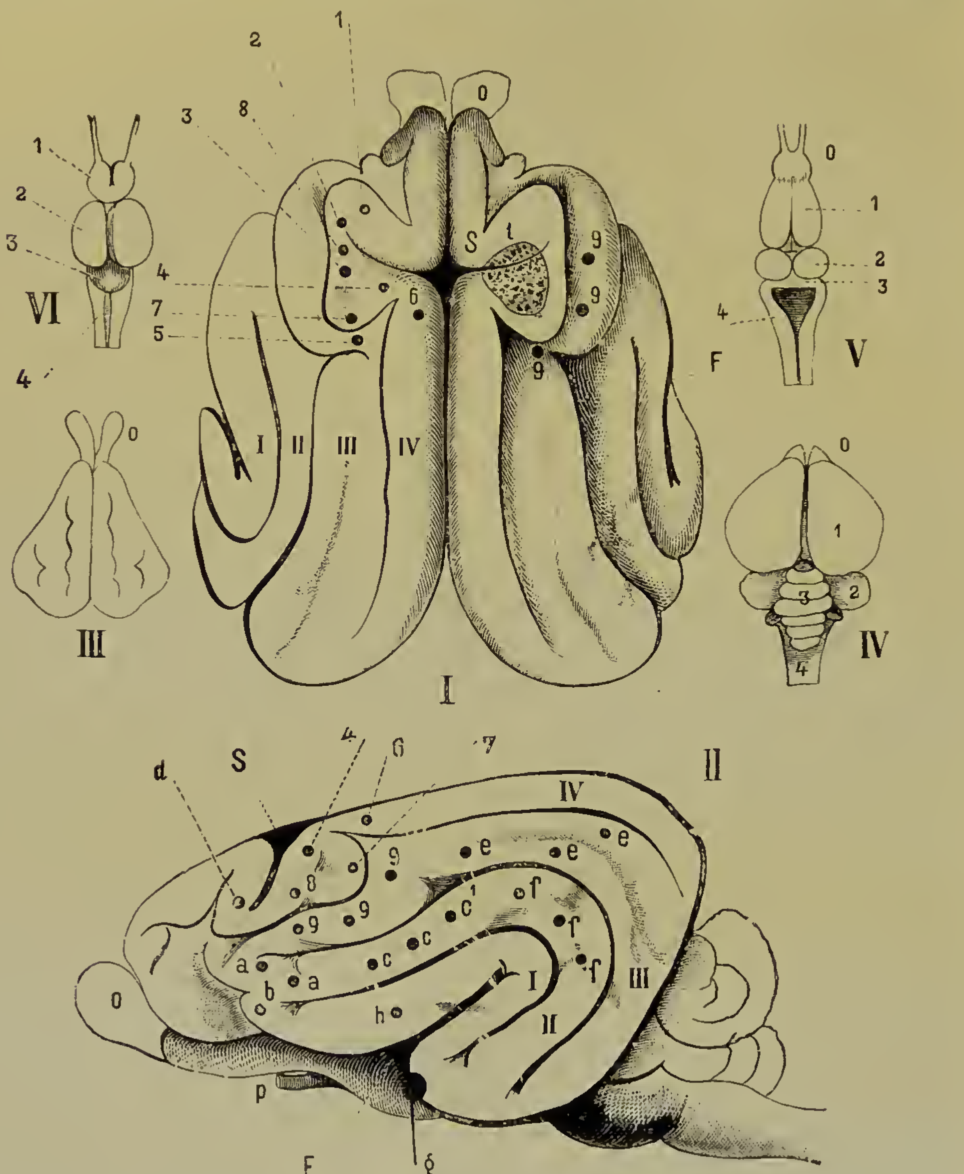


Fig. 609.

I, Cerebrum of the dog from above ; II, from the side ; I, II, III, IV, the four primary convolutions,—S, sulcus cruciatus ; F, Sylvian fossa ; *o*, olfactory lobe ; *p*, optic nerve ; 1, motor area for the muscles of the neck ; 2, extensors and abductors of the fore limb ; 3, flexors and rotators of the fore limb ; 4, the muscles of the hind limb ; 5, the facial muscles ; 6, lateral switching movements of the tail ; 7, retraction and abduction of the fore limb ; 8, elevation of the shoulder and extension of fore limb (movements as in walking) ; 9, 9, orbicularis palpebrarum, zygomaticus, closure of the eyelids. II, *a*, *a*, retraction and elevation of the angle of the mouth ; *b*, opening of the mouth and movements of the oral centre ; *c*, *c*, platysma ; *d*, opening of the eye. I, *t*, thermic centre, according to Eulenburg and Landois. III, cerebrum of the rabbit from above ; IV, cerebrum of the pigeon from above ; V, cerebrum of the frog from above ; VI, cerebrum of the carp from above—(in all these *o* is the olfactory lobe ; 1, cerebrum ; 2, optic lobe ; 3, cerebellum ; 4, medulla oblongata).

elevation of the shoulder and extension of the fore limb, as in walking ; the area marked

9, 9, 9, controls the movements of the orbicularis palpebrarum, and of the zygomaticus (closure of the eyelids), together with the upward movement of the eyeball and narrowing of the pupil. Stimulation of the areas *a*, *a* (fig. 11) is followed by retraction and elevation of the angle of the mouth, with partial opening of the mouth; at *b*, Ferrier observed opening of the mouth with protrusion and retraction of the tongue, while the dog not unfrequently howled. He called this centre the "*oral centre.*" Stimulation of *c c* causes retraction of the angle of the mouth, owing to the action of the platysma, while *c′* causes elevation of the angle of the mouth and of one-half of the face, until the eye may be closed, just as in 9. Stimulation of *d* is followed by opening of the eye and dilatation of the pupil, while the eyes and head are turned towards the other side. According to H. Munk, the prefrontal region has an influence upon the attitude of the body (?). The perineal muscles contract when the gyrus postcruciatus is stimulated. Stimulation of the gyrus præcruciatus on its anterior and sloping aspect causes movements in the pharynx and larynx.

[The motor areas in the **dog** are not very sharply defined, and indeed they may overlap somewhat, so that the localisation of representation of movement in the dog's cortex is much less perfect than in the higher animals, *e.g.*, monkey. In the **rabbit** and still lower vertebrates the localisation is still less precise and more diffuse.]

[Experiments on **monkeys** indicate that in them the motor areas are more sharply defined from each other, and that there is a great differentiation of representation of movement in the cortex of the anthropoid apes as compared with the dog. In man this differentiation of the representation of movements appears to be more precise still.]

[In **birds**, such as the dove and hen, the limb muscles do not appear to be represented in the cortex, but in the owl and hawk there is representation of the hind limbs in the cortex (*Schräder*).]

The position of the individual motor areas may vary somewhat, and they may be slightly different on the two sides (*Luciani and Tamburini*).

Strong Stimuli.—If the stimulation be very strong, not only the muscles on the opposite side, but those on the same side, may contract. These latter movements belong to the class of associated movements, and are due to conduction through commissural fibres. Those muscles, which usually (muscles of mastication) or always (muscles of eye, larynx, and face) act together, appear to have a centre not only in the opposite but also in the hemisphere of the same side (*Exner*). [All observers have found that stimulation of the facial centre causes identical (associated) movements on *both* sides of the face, so that both sides of the face seem to be represented in each hemisphere. Schäfer and Horsley's experiments make it very probable that some other muscles, *e.g.*, some of the trunk muscles, pectorals, and recti abdominis, are represented bilaterally in the hemispheres. This is an important point in relation to recovery after the supposed destruction of a centre, and has an intimate bearing on the question of "Substitution," in reference to the restoration of nerve-function (p. 843).]

Strong stimulation of the motor regions may give rise in dogs to a complete general convulsive **epileptic attack**, which usually begins with contractions of the groups of muscles especially related to the stimulated centre (*Ferrier, Eulenburg and Landois, Albertoni, Luciani and Tamburini*); then often passes to the corresponding limb of the opposite side (associated movements); and lastly, all the muscles of the body are thrown into tonic and then into clonic spasms. The opposite side of the body has been observed to pass into spasms from below upwards, after the contractions were developed in the other side. The spasmodic excitement passes from centre to centre, an intermediate motor region never being passed over. After this condition has once been produced, the slightest stimulation may suffice to bring on a new epileptic attack (§ 373). During the attack the cerebral circulation is accelerated. According to Eckhard and Danillo, epileptic attacks cannot be discharged from the posterior part of the cerebrum by means of weak currents. Stimulation of the **sub-cortical** white matter causes epilepsy, which, however, begins in the muscles of the *same* side (*Bubnoff and Heidenhain*). These contractions are due to an escape of the electrical current, which thus reaches the medulla oblongata (§ 373).

Mechanical stimulation, *e.g.*, scraping the motor areas for the limbs, produces movements in these parts (*Luciani*).

Cerebral Epilepsy.—It is of great practical diagnostic importance to ascertain if stimulation of the motor areas in man, due to local diseases (inflammation, tumours, softening, degenerative irritation), causes movements. [Hughlings-Jackson has shown that local diseases of the cortex may cause spasmodic contractions in certain groups of muscles, a condition known as "**Jacksonian Epilepsy,**" and he explains in this way the occurrence of unilateral local epileptiform spasms, which were observed by Ferrier and Landois to occur after inflammatory irritation.] Luciani observed these spasms in dogs, and sometimes they were so violent and general as to constitute an attack of epilepsy. This condition became hereditary, and the animals ultimately died from epilepsy (§ 373). According to Eckhard, epileptic attacks are never produced by stimulation of the surface of the posterior convolutions. [In passing from apes to carnivora, epilepsy as a result of electrical stimulation of the cortex is far more readily produced in the latter animals than in the former. Indeed, in the Orang, Beevor and Horsley never observed epilepsy to follow excitation of any part of the cortex.]

If certain motor areas are **extirpated**, the epileptic attack is absent from the muscles controlled by these areas (*Luciani*). Separation of the motor cortical area by means of a horizontal section *during* an attack cuts short the latter (*Munk*). During an epileptic attack it is possible to excise the motor area of one extremity, and thus exclude this limb from the attack whilst the rest of the body is convulsed.

Drugs.—The continued use of *potassium bromide* prevents the production of epilepsy on stimulating the cortical areas.

Chemical Stimulation.—Substances such as occur in urine, *e.g.*, kreatinin, kreatin, acid potassic phosphate, and sediment of urates, when sprinkled on the motor areas of the dog, cause pronounced eclampsic, *clonic convulsions*, which recur spontaneously, and are followed by deep coma. These symptoms are like those of uræmic poisoning. The sensory centres, especially that for vision, seem also to be affected by chemical stimulation (*Landois*).

[**Motor Centres in the Monkey.**—Ferrier has mapped out a large number of centres on the outer surface of the brain in the monkey, and to each centre he has given a number. These numbers have been transferred to corresponding convolutions on the human brain, numbered accordingly. These areas are specially distributed on the convolutions around the fissure of Rolando, including in the monkey the posterior extremities of the posterior and middle frontal convolutions, the ascending frontal, ascending parietal, and part of the parietal lobule.]

[**Areas mapped out by Ferrier.**—Fig. 610 represents these areas transferred to the corresponding areas in **man.** (1) On the superior parietal lobule (advance of the opposite hind limb, as in walking. (2), (3), (4) Around the upper extremity of the fissure of Rolando (complex movements of the opposite leg and arm, and of the trunk, as in swimming). (*a*), (*b*), (*c*), (*d*) On the ascending parietal or posterior central convolution (individual and combined movements of the fingers and wrist of the opposite hand or prehensile movements). (5) Posterior end of the superior frontal convolution (extension forward of the opposite arm and hand). (6) Upper part of the ascending frontal or anterior central convolution (supination and flexion of the opposite fore-arm). (7) Middle of the same convolution (retraction and elevation of the opposite angle of the mouth). (8) At the lower end of the same convolution (elevation of the ala nasi and upper lip, and depression of the lower lip on the opposite side). (9), (10) Broca's convolution (opening of the mouth with protrusion and retraction of the tongue—aphasic region). (11) Between 10 and the lower end of the ascending parietal convolution (retraction of the opposite angle of the mouth, the head turns towards one side). (12) Posterior part of the superior and middle frontal convolutions (the eyes open widely, the pupils dilate, and the head and eyes turn towards the opposite side). (13), (13′) Supra-marginal and angular gyrus (the eyes move towards the opposite side, and upwards or downwards—centre of vision). (14) Superior temporo-sphenoidal convolution (pricking of the opposite ear, pupils dilate, and the head and eyes turn to the opposite side—hearing centre).]

[**Experiments on Monkeys.**—Electrical stimulation of the anterior part of the frontal lobes yields negative results: but behind the anterior end of the sagittal limb of the precentral sulcus there are lateral movements of the head and eyes.

If the anterior third or fourth be removed, Schäfer and Horsley observed no motor paralysis nor any deficiency of general or special sensibility. Excitation of the **external surface** (*motor area*) led Ferrier to map out the areas named on p. 862. Schäfer and Horsley's experiments agree with Ferrier's, and they map out the motor area into a number of main areas, each of which is particularly concerned with the movement of a particular part or limb, and in some of which centres con-

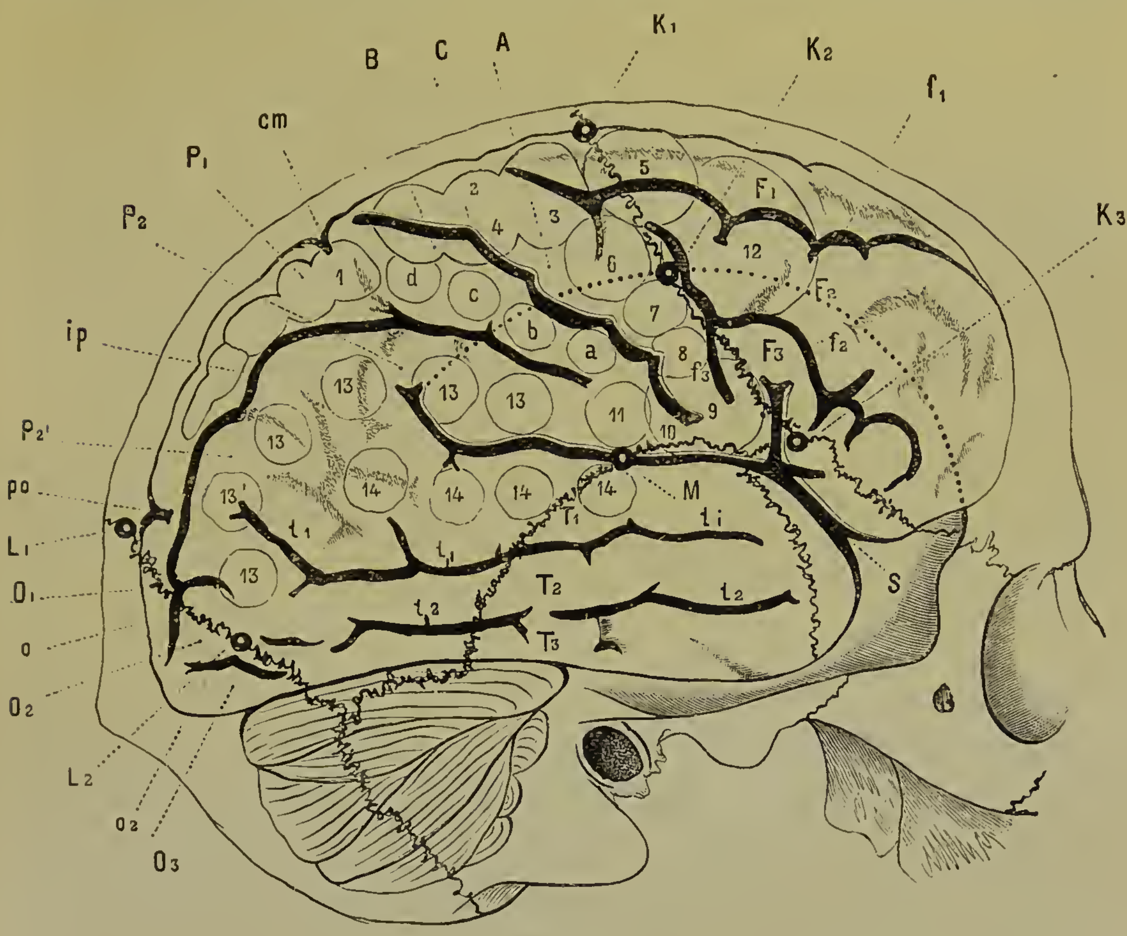


Fig. 610.

The brain with the chief convolutions (after *Ecker*). See also figs. 624, 625 in their relation to the skull. The numbers 1 to 14, and the letters *a* to *d*, indicate cortical areas (p. 862). S, Sylvian fissure; C, central sulcus, or fissure of Rolando; A, anterior, and B, posterior central convolutions; F_1, upper, F_2, middle, and F_3, lowest frontal convolutions; f_1, superior, and f_2, inferior frontal fissure; f_3, sulcus præcentralis; P_1, superior, P_2, inferior parietal lobe, with P_2, gyrus supra-marginalis; $P_2{}^1$, gyrus angularis; *ip*, sulcus inter-parietalis; *cm*, end of calloso-marginal fissure; O_1, O_2, O_3, occipital convolutions; *po*, parieto-occipital fissure; T_1, T_2, T_3, temporo-sphenoidal convolutions; K_1, K_2, K_3, points in the coronal suture; λ_1, λ_2, in the lambdoidal suture.

cerned with more specialised movements may be marked out. The arm-area is roughly triangular (fig. 611), and "occupies most of the upper half of the ascending parietal and ascending frontal gyri, from a little beneath the level of the sagittal part of the precentral fissure below, nearly to the margin of the hemisphere above, together with the adjacent part of the frontal lobe below the small antero-posterior sulcus." It bends round and is continuous with a part of the marginal gyrus. The special movements of the arm are indicated in fig. 611.]

Within any particular area there is motor representation of the movements capable

of being executed by the corresponding muscles. Thus in the arm-area the movements represented are from above downwards, those at the **shoulder**, **elbow**, **wrist**, **digits**, and **thumb**, and of course all the complex combinations of movements which these parts can execute.]

[The **face-area**, lying ventral to the arm-area, gives rise not only to movements of the facial muscles, but also of the whole of the upper end of the alimentary tube. It comprises the whole of the ascending parietal and frontal convolutions below the arm-area, down to the fissure of Sylvius, and including the external surface of the operculum. As is shown in fig. 611, at the upper part of the area the **eyelids** are represented, below or ventral to this curve successively the movements of the **mouth**, **tongue**, those for **mastication** and **swallowing**, and at the lower or ventral end of the ascending frontal convolution is the area for the **larynx** and phonation (p. 865).]

[The **head-area**—*i.e.*, for movements of the head brought about by the muscles of the neck—or area for visual direction—comprises part of the frontal lobe from

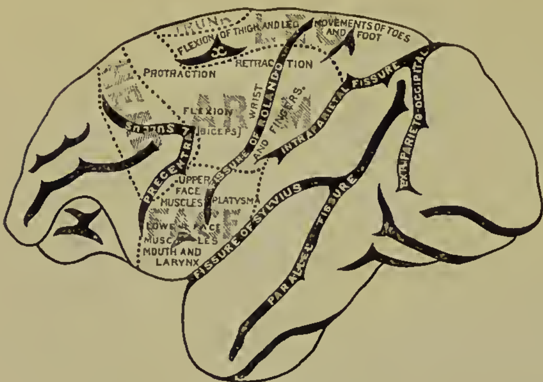


Fig. 611.

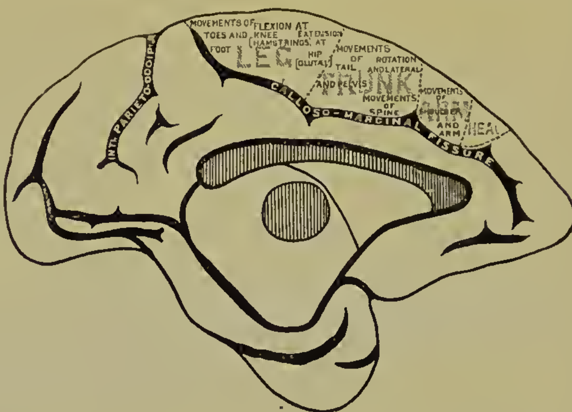


Fig. 612.

Fig. 611.—Diagram of the motor areas on the outer surface of a monkey's brain (*Horsley and Schäfer*. Fig. 612.—Diagram of the motor areas on the marginal convolution of a monkey's brain (*Horsley and Schäfer*).

the margin of the hemisphere to the face-area. In front it is bounded by the non-excitable part of the frontal lobe. Its stimulation gives the results obtained by Ferrier on stimulating his No. 12 centre. Occupying the ventral part of the head-area on the posterior extremity of the middle frontal convolution—*i.e.*, in front of the precentral sulcus—is the area for the movements of the **eyeballs** or "area for the **eyes**" (fig. 611).]

[The **leg area**, or "**area for the hind limb**," is partly situate on the mesial surface—*i.e.*, the marginal convolution—but it extends over to the external surface from the parieto-occipital fissure nearly to the level of the anterior end of the small sulcus marked LEG (fig. 607). Within this area are to be distinguished from before backwards special areas for the **hip**, **knee**, **ankle**, **hallux**, and **digits**.]

[The **trunk-area** scarcely extends over the margin to reach the external surface. It exists on the marginal convolution lying between the area for the head in front, and that for the leg behind.]

[Schäfer and Horsley have extended Ferrier's researches, and shown that motor centres exist in the **marginal convolution** (fig. 612), which is excitable only in that portion corresponding in extent (antero-posteriorly) to the excitable portion of the outer surface of the hemisphere. Anteriorly it reaches forward to a line which is opposite the junction of the posterior and middle thirds of the superior frontal convolution (centre 12), while posteriorly it extends backwards opposite to the parietal lobule, including the paracentral lobule, which contains large multi-

polar pyramidal motor cells. The rest of the mesial surface is inexcitable. They find that the centres are arranged from before backwards in the following order:—(1) Movements of the head—this area is very small, and belongs to the large head-area on the external surface; (2) of the fore-arm and hand; (3) of the arm at the shoulder; (4) of the upper dorsal part of the trunk; (6) of the leg at the hip; (7) of the lower leg at the knee; (8) of the foot and toes.]

[Just as there are differences in motor representation in the cortex as we descend in the animal scale, so there are differences amongst animals belonging to the same group, *e.g.*, monkeys. Comparing a Macacque monkey with an Orang, it is difficult to get single primary movements uncomplicated by movements of other parts on stimulation of the cortex of a Macacque monkey, but in the Orang single primary movements are readily obtained, and this seems to demonstrate the great advance in evolution of function in the Orang's cortex above that of the Macacque. Moreover, in the Orang, instead of the excitable area of the cortex being continuous, as in the Macacque, it is in the Orang much interrupted by spaces from which no effect can be obtained even by the application of strong stimuli. Thus excitable areas are separated from each other by inexcitable areas. Direct observation has shown that for certain centres at least a similar interrupted mode of representation exists in man (*Beevor and Horsley*). It appears in addition that motor representation in the cortex is found only on the summits of the gyri of the convoluted surface, while at a sulcus it is inexcitable.]

Excitation of the Area AS produces movements of the arm (fig. 615). These vary according to the spot stimulated, but towards the anterior part of the area, movements of the wrist and fore-arm, towards the posterior part movements of the arm and shoulder, are more frequently the result of the excitation. Excitation of **Tr** produces movements of the trunk, generally arching and rotation. Those movements which are called forth by stimulating the anterior part of the area are usually confined to the upper part of the trunk (thoracic region), and are often associated with movements of the shoulder and arm; those called forth by stimulating the posterior part are movements of the abdominal and pelvic regions and of the tail, and are often associated with movements of the hip and leg. Excitation of the area **L** produces movements in the lower limb. These vary according to the part stimulated, extension of the hip being especially associated with excitation of the anterior part of the area, and contraction of the hamstrings with excitation of the middle part.]

[**Motor Representation of the Larynx.**—In this connection we must remember that the larynx subserves the two purposes of respiration and phonation. The bulb is the main seat of respiration, and recent researches by Krause, Horsley, and Semon show that there seems to be independent representation of the larynx in the bulb for respiratory laryngeal movements, and independent of that for thoracic movements. Moreover, the larynx is independently represented in the bulb for the movements of phonation; thus a purely reflex cry is produced in animals after removal of the cerebrum, and stimulation of one side of the bulb near the calamus scriptorius causes adduction of the vocal cord on the same side. Perhaps the abductors and adductors are represented independently.

In the cortex cerebri the representation of the larynx seems to be independent of that of respiration, and amongst animals the cat has the greatest, the monkey the least development of representation in the cortex, while the respiratory movements are also represented in the cortex.]

[Horsley and Semon find that "there is in each cerebral hemisphere an area of bilateral representation of adductor movements of the vocal cords, situated in the monkey just posterior to the lower end of the præcentral sulcus at the base of the third frontal gyrus, and in the carnivora in the præcrucial and neighbouring gyrus. This area has a focus of intensest representation in the anterior half of the foot of the ascending frontal convolution. Stimulation of this point produces complete bilateral adduction of the vocal cords, which lasts as long as the stimulation is continued." Thus unilateral stimulation produces a bilateral effect, so that with bilateral representation of both sides of the larynx in one hemisphere, excision of that centre does not necessarily produce unilateral paralysis of a vocal cord; indeed, the phonatory centre and even one hemisphere has been

excised, yet on stimulation of the remaining phonatory cortical area bilateral adduction occurs. The fibres from the cortical area run in the corona radiata, those for respiration run first in the anterior limb of the internal capsule, and at a lower plane in the region of the genu. Those that subserve phonation, and excitation of which produces adduction of the vocal cords, are grouped just posterior to the genu (cat), and at a lower plane in the posterior limb. These fibres proceed to form connections with the bulbar laryngeal apparatus (*Horsley and Semon*).]

[It will be noticed that the areas are spoken of in terms of the part of the body which is affected by the stimulation of a particular area. There is reason for believing, however, that what is represented in the cerebral cortex is not mere muscular mass, but rather the variety and complexity of movements capable of being executed by these muscles. Thus one speaks not of representation of the muscles in the motor areas, but of "representation of muscular movements." This view is supported by a study of the relative size of certain motor areas as compared with the size of the area of the body which such areas represent. Thus the thumb area is relatively far larger than that of the shoulder or area for the hip, but the difference is explained by the great complexity of movements executed by the thumb as compared with the simpler movements of the shoulder.]

[**Do similar Centres exist in Man?**—The results of clinical and pathological investigations show that similar, although not absolutely identical, areas exist in man. The motor areas, or those which have a special relation to voluntary motion in man, exist in part in the convolutions bounding the fissure of Rolando, and occupy the "**central convolutions,**" *i.e.*, the ascending frontal and ascending parietal convolutions along with the superior parietal lobule, and along the mesial surface of the hemisphere, the paracentral lobule, and precuneus (fig. 614). In this region the upper third of the ascending frontal and parietal convolutions, along with the superior parietal, are the **leg** area (fig. 614, LEG), the middle third of the ascending parietal and ascending frontal for the **arm**, and the upper part of the lowest third of these convolutions for the **face**, while the very lowest part of the ascending frontal convolution is the area for the movements of the **lips** (LIPS) and **tongue** (T). (Compare figs. 611, 616.) The last area, with the posterior extremity of the third left frontal convolution, is the centre for voluntary **speech.** We cannot say whether these "centres" are sharply mapped off from each other. In any case a very strong stimulation of one centre may involve an adjacent area. So far as is yet known, centres Nos. 5 and 12, as represented in the monkey's brain—those on the posterior extremity of the superior and middle frontal convolutions,—(5) for extension forward of the arm and hand, and (12) for opening the eyes and turning the head towards the opposite side (as in surprise), are not represented in the human brain. So accurately have certain of these areas been located, that surgeons, in suitable cases, have been able not only to diagnose the position of a tumour causing certain symptoms, but also to excise it.]

Bilateral Movements.—Movements in both sides of the body following upon excitation of one hemisphere are common, but many of these movements cannot be claimed as examples of strictly bilateral representation in the cortex. The movements of the trunk (rectus, abdominis, &c.), tongue, turning the head, and conjugate deviation of the eyeballs are often classed as such, but in reality they are not so. The movements of pouting of the lips, mastication, swallowing, and movements of the soft palate, adduction of the vocal cords seem to be truly bilateral movements (*Beevor and Horsley*).]

[We may, therefore, assert as a general proposition that the muscles of one lateral half of the body are regulated by certain areas in the opposite cerebral hemisphere, except in the case of bilateral muscles usually acting together.]

[Gowers maintains that the motor region is not exclusively motor, but that destruction of this area also leads to some loss of sensation. Starr also asserts that perceptions occur in the grey matter of the cortex of the "central" region and parietal convolutions, and that the various sensory areas for the various parts of the body lie about, and coincide to some extent with, the

motor various areas for similar parts, but the sensory area is more extensive than the motor area, extending into the parietal behind the motor area, which is confined to the ascending frontal and parietal convolutions.]

II. Method of Destruction or **Ablation of Parts of the Cortex.**—Much confusion in this matter has arisen from comparing the results obtained on animals of different species. [It seems quite certain that the results obtained in the dog are quite different from those in the monkey. The motor areas may be simply excised with a knife, or the surface of the brain may be washed away with a stream of water, as was done by Goltz in dogs.]

[In the **dog**, the areas which are described as motor may be removed either by the knife (*Hermann*) or by means of a stream of water so directed as to wash away the grey matter (*Goltz*). In both cases, although there was some paralysis on the opposite side of the body, this was but temporary, for the paralysis disappeared within a few days, the animals having very decided control over their muscles, although Goltz admits that certain acts, especially those which the dogs had been trained to execute, *e.g.*, giving a paw, were executed "clumsily," indicating some failure of complete control, which Goltz ascribed to loss of tactile sensibility. Goltz thinks that the *extent* of the injury has more to do with the result than the locality. The restoration of motion was not due to the action of the corresponding centre of the opposite side, as destruction of this centre, although it produced the usual symptoms on the side which it governed, had no effect on the previous result (*Carville and Duret*).]

[In the **monkey**, the experiments of Ferrier tend to show that destruction of a motor centre, *e.g.*, that for the arm, results in *permanent* paralysis of the arm of the opposite side, and if the centres for the arm and leg are destroyed, there is permanent hemiplegia of the opposite side. "In order that the hemiplegia or paraplegia produced by cortical ablation shall be complete, it is necessary to include the part of the marginal gyrus corresponding in longitudinal extent to the excitable areas of the external surface." The amount of paralysis produced by ablation of the marginal gyri alone is as great as that caused by removal of the much more extensive external areas; but the complexity of the muscular movements which are governed from these areas is much greater than in those governed from the marginal gyrus (*Schäfer and Horsley*).]

[In **man**, records of destructive lesions of the motor areas in whole or part have now accumulated to such an extent as to leave no doubt that if there be, say, a destructive lesion of the middle third of the cortex of the ascending frontal and ascending parietal convolutions, there will be paralysis of the arm of the opposite side; and the same is true for the other centres.]

[In **extirpation** or **ablation of the motor centres**, again, much confusion has arisen from comparing the results obtained on different animals. In the dog there is no permanent motor paralysis, in the monkey and man there is. The difference is this, that in the dog the lower centres, perhaps the basal ganglia, are able to subserve the execution of those co-ordinated movements required for standing, progression, &c. As we proceed higher in the animal scale, the motor cortical centres assume more and more of the functions subserved by the basal ganglia in lower animals. There is, as it were, a gradual displacement of motor centres connected with volitional motor acts to the cortical region, as we ascend in the zoological scale.]

Differences in Animals.—The higher the development of the intelligence of animals, the more have their movements been learned, and the more have they gradually come to be controlled by the will; in them the disturbance of the motor phenomena becomes more pronounced and persistent after destruction of the cortical psychomotor centres. Whilst in the lower vertebrates, including the **birds**, extirpation of the whole hemispheres does not materially interfere with movements, the co-ordinated reflex movements being sufficient—in **dogs** occasionally, but exceptionally, extirpation of several motor areas produces visible permanent disturbance of motor acts—and in **monkeys** and **man** (§ 378) the paralytic phenomena may be intense and persistent.

Acquired Movements.—Among the movements performed by man are many which have been acquired after much practice, and have been subjected to voluntary control, *e.g.*, the movements of the hands for many manual occupations. After a lesion of certain motor areas, such

movements are reacquired only very slowly and incompletely, or it may be not at all. [The interference with these finer acquired movements sometimes becomes very marked in lesions of the motor areas produced by hæmorrhage, and in some cases of hemiplegia.] Those movements, however, which are, as it were, innate [or as they are sometimes termed **fundamental**, in opposition to acquired], and are under the control of the will without much practice—such as the associated movements of the eyes, face, some of those of the limbs—are either rapidly restored after the lesion, or they appear to suffer but slightly after a lesion of the cerebral cortex; the facial muscles are never so completely paralysed as from a lesion of the trunk of the facial nerve; usually the eye can be closed in the former case. The movements necessary for sucking have been performed by hemicephalic infants.

Theoretical.—Hitzig ascribes the disturbance of movement, after the removal of the motor centres, to the loss of the "*muscular sensibility*." Schiff refers it to the loss of *tactile sensibility*. According to Ferrier, the tactile and sensory impressions are not appreciably diminished or altered. The descending degeneration of the pyramidal tracts in the lateral columns, according to Schiff, occurs after section of the posterior half of the cervical spinal cord, or even after section of the posterior part of the lateral columns. After dividing the latter, and allowing secondary degeneration to take place, it is not possible to discharge movements by stimulating the cortex cerebri. [Schiff divided the posterior column of the cord, and found that stimulation of the opposite motor cortex failed to excite movements in the opposite fore limbs. He supposed that this result was due to ascending degeneration. Horsley finds, however, that Schiff's results are due to transverse aseptic myelitis at the seat of operation, thus causing a "block" there in the motor tract.] The posterior columns, and their continuation upwards to the brain, are supposed to carry the impulses upwards to the cerebrum (ascending the limb of the reflex arc), where, after being modified in the centres, they are carried outwards by the pyramidal tracts (descending limb of the reflex arc). [Some hold that the posterior columns are directly connected with the cortical motor area, while others think that a sensory perceptive centre is interposed between the afferent and efferent impulses.] Between, but deeper in the brain, lie the centres for tactile sensibility. Landois and Eulenburg observed in a dog, from which the motor centres for the extremities had been removed on *both* sides, that the movements became completely *ataxic*, *i.e.*, the animal could not execute such co-ordinated movements as walking, standing, &c. Goltz regards the disturbances of movement after injury of the cortex as due to inhibition. Schiff maintains that when the cortex cerebri is stimulated we do not stimulate a cortical centre, but only the sensory channels of a reflex arc, the continuation of the posterior columns, so that on this supposition the movements resulting from stimulation of the motor points would be reflex movements. The centres lie deeper in the brain. This view is not generally entertained.

Modifying Conditions.—The excitability of the motor centres is capable of being considerably modified. [In deep **ether-narcosis**, stimulation of the motor region of the cortex does not produce contraction, but stimulation of the subjacent white matter does.] Stimulation of sensory nerves diminishes it; thus, the curve of contraction of the muscles becomes lower and longer, while the reaction-time is lengthened simultaneously. Only when, owing to strong stimulation, the reflex muscular contractions are vigorous, the excitability of the cortical centres appears to be increased. Specially noteworthy is the fact that, in a certain stage of **morphia-narcosis**, a stimulus which is too feeble to discharge a contraction becomes effective at once, if immediately before the stimulus is applied to the cortical centre, the skin of certain cutaneous areas be subjected to gentle tactile stimulation. When *strong* pressure is applied to the foot, the contractions become tonic in their nature, so that all stimuli, which under normal conditions produce only temporary stimulation, now stimulate these centres continuously. If, during the tonic contraction, during morphia-narcosis, one gently strokes the back of the foot, blows on the face, gently taps the nose, or stimulates the sciatic nerve, suddenly relaxation of the muscles again occurs. These phenomena call to mind the analogous observations in hypnotised animals (§ 374). [Sub-minimal stimuli applied to a centre fail to excite movement, but sometimes if the skin over the muscle corresponding to the area stimulated be gently stroked, contraction may take place. These results seem to show how complex volitional motor acts are, and that they have some relation to afferent impulses arising in cutaneous surfaces.] Another very remarkable observation is, that when either owing to a reflex effect, or to *strong* electrical stimulation of a cortical centre, contraction of

the corresponding muscles is produced, then *feeble* stimulation of the same centre, but also of other centres, suppresses the movement. Thus, we have the remarkable fact that, according to the strength of the stimulus applied to the motor apparatus, we can either produce movement or suppress a movement already in progress (*Bubnoff and Heidenhain*).

[**Excision of the Thyroid** affects the nerve-centres. After thyroidectomy (twenty-four hours) the tetanus obtained by stimulating the cortex is greatly changed. It ceases when the stimulating current is shut off, as suddenly as that observed on stimulating the corona radiata. In more advanced cases, the tetanus is soon exhausted, and is often followed by clonic epileptoid spasms. In the latter stages, after thyroidectomy, there may be only a feeble tetanus, or none at all, on stimulating the motor areas, so great is the state of depression of function of these centres (*Horsley*). Actual structural changes take place in the central nervous system, and Autokratoff concludes that, in the absence of the thyroid, a poison accumulates in the organism, and acts specially on the nervous system.]

[Warner has directed attention to **visible muscular movements** apart from those studied in epilepsy, chorea, athetosis—and including attitude, gait, movements of the eyeballs, position of the hand, and posture in general, &c.—as **expressive of states of the brain** and nerve-centres.]

[**Electrical Variations accompanying cerebral action.**—That an impulse is conducted along the pyramidal tracts when the motor areas are stimulated was proved by Gotch and Horsley. By means of non-polarisable electrodes applied, one to the transverse section of the cord in the lower dorsal region, and the other a little higher up on the longitudinal surface of the cord, they led off to an electrometer the current thus obtained from the cord. They found on stimulating the area for the hind limb in the cortex that they obtained a negative variation of the cord current, or, in other words, a current of action; but no current was obtained when other parts of the cortex were stimulated. If from stimulation of any area other than the leg area, epilepsy happened to be produced, then currents of action were noted in the lower dorsal region, and moreover, the oscillations of the mercury of the electrometer corresponded to the type of muscular contraction, *i.e.*, whether the contractions were tonic or clonic. It seems evident, therefore, that when the motor regions of the cortex are excited, nervous impulses accompanied by "currents of action" are transmitted downwards along the pyramidal tracts.]

[Beck and Fleischl have recently asserted that afferent impulses passing to the cerebral areas lead to a negative variation of the nerve-current of the cortex cerebri. Caton, in 1875, described electrical currents of the cortex cerebri.]

376. SENSORY CORTICAL CENTRES.—[There must be some connection between the surface of the brain and the afferent channels through which **sensory impulses** pass inwards, and although the channels for sensory impulses are, perhaps, not so definitely localised as those for voluntary motion, still we know that sensory impulses for the opposite half of the body travel upwards through the posterior third of the posterior limb of the internal capsule (fig. 626, S), to radiate in all probability into the occipital and temporo-sphenoidal lobes. Parts of these convolutions are sometimes spoken of as "**sensory centres**" or "psycho-sensorial" areas.]

[The same **methods** have been applied to the investigation of these centres, viz., stimulation and extirpation. **Stimulation.**—Ferrier found that electrical stimulation of the angular gyrus (monkey) caused movements of the eyeballs towards the side, with sometimes associated movements of the head, but he regarded these as reflex movements, so that for this and other reasons he, in his earliest contributions, considered the angular gyrus and adjacent parts as the "centre for vision." On stimulating the first temporo-sphenoidal convolution, the monkey pricked the opposite ear, the pupils dilated, while the head and ears turned to the opposite side; it exhibited movements similar to those caused by a loud sound: these movements are also reflex phenomena, so that he located the "auditory centre" in this region, and on somewhat similar grounds. As the result of inferences from the stimulation and extirpation of other parts, he referred the centres for smell and taste to the tip of the temporo-sphenoidal lobe, and for touch to the hippocampus major, but all these statements have not been confirmed.]

[Goltz experimented on dogs by **washing away** the cortex cerebri, and found that when a

sufficient amount of the grey matter is removed, and after recovery from the immediate effects of the operation, there is a peculiar defect of vision and other sensory defects, but so far Goltz has not found that there is any difference in this respect between removal of the anterior and posterior lobes of the dog's brain. The dog is not blind, as it can see and use its eyes to avoid obstacles, but it seemed as if the animal failed to recognise food or flesh *as such*, when placed before it; while exhibitions, which, before the operation, greatly excited the dog, ceased to do so. Goltz caused his servant to dress himself in a mummer's red-coloured garb, which previously had greatly excited the dog, but after the operation the dog, although it was not blind, was no longer excited thereby. Nor was it afterwards cowed by the appearance of a whip. After a time there was recovery to a certain extent if the animal was trained, whether by the deposition of new impressions, or by opening up new channels, or by the partial recovery of some parts of the grey matter not removed, it is impossible to say.]

[Munk has mapped out the surface of the brain into a series of "sensory" or psycho-sensorial centres, but he distinguishes between complete and total extirpation of these centres and the phenomena which follow these operations.]

When these *centres* are *partially* disorganised, the mechanism of the sensory activity may remain intact, but "the conscious link is wanting." A dog with its centres thus destroyed, sees, hears, or smells, but it no longer knows what it sees, hears, or smells. These centres are in a certain sense the seat of experience that has been acquired through the organs of sense. **Stimulation** of these centres may give rise to movements, such as occur when sudden intense sensory impressions are produced. These movements are in no way to be confounded with the movements which result from direct stimulation of the motor cortical centres. To this group of movements belong dilatation of the pupil and the fissure of the eyelids, as well as lateral movements of the eyeball.

1. "**The visual area**," according to Munk, embraces the outer convex part of the occipital lobe of the dog's brain. [This area and its connections are represented in fig. 613. It is, therefore, in the area supplied by the posterior cerebral artery. In all probability, however, it also embraces the mesial aspect of the occipital lobe including the cuneus (fig. 607).] If the occipital lobes be completely destroyed, the dog remains permanently blind ("**cortical** or **absolute blindness**"). If, however, only the central circular area be destroyed, there is loss of the conscious visual sensation, which may be called "**psychical blindness**" (*Munk*) [a condition of visual defect like that observed by Goltz in the dog, in which the dog saw an object, *e.g.*, its food, but failed to recognise it as such. There is a certain amount of recovery if the whole visual area be not removed. According to Schäfer, the visual area of the cerebral cortex in the monkey comprises the whole of the occipital lobe, and perhaps a part of the angular gyrus. He finds, with Munk, that removal of one occipital lobe is followed by **hemianopia**, *i.e.*, blindness in the lateral half of each retina corresponding to the side operated on. The blindness passes off. Removal of both occipital lobes is said to produce total and permanent blindness, whereas destruction of the cortex of both angular gyri is not followed by any appreciable permanent defect of vision. Ferrier, however, does not accept these statements.]

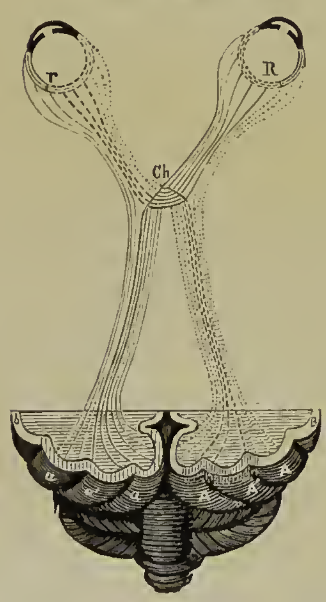


Fig. 613.
Course of the psycho-optic fibres (after *Munk*).

[Ferrier and Yeo find that after operations conducted antiseptically, removal of both occipital lobes (monkeys) does not cause any recognisable disturbance of vision, or other bodily or mental derangement, provided the lesion does not extend beyond the parieto-occipital fissure. Nor does destruction of both angular gyri

cause permanent loss of vision; such loss of vision lasts only three days, so that in Ferrier's original experiments the animals lived for too short a time after the operation to enable a just conclusion to be arrived at. Destruction of both angular gyri and occipital lobes causes total and permanent blindness in both eyes in monkeys, without any impairment of the other senses or motor power. This region Ferrier calls the "occipito-angular region."

[**Stimulation** of the **angular gyrus** causes movements of the eyes to the opposite side, with closure of the eyelids and contraction of the pupil. The eyeballs were directed upwards or downwards according as the electrodes were applied to the anterior or posterior limb of the angular gyrus (*Ferrier*). Stimulation of the whole of the cortex of the occipital lobe, including its mesial and under surfaces, causes conjugate deviation of the eyes to the opposite side, the direction of movement varying with the position of the electrodes.]

Mauthner denies the existence of cortical blindness, and believes that, after destruction of the middle of the visual centre, the reason why the dog does not recognise the object with the opposite eye is because, owing to there being only indirect vision, there is no distinct impression on the retina. The position of the visual centre has been variously stated by different observers. According to Ferrier, in the dog it lies in the occipital part of the III primary convolution, near the spots marked *c*, *c*, *c*, in fig. 609; according to his newer researches, in the occipital lobe and gyrus angularis.

Connection with the Retina.—Munk asserts that in dogs *both* retinæ are connected with each visual cortical centre, and in such a manner that the greatest part of each retina is connected with the *opposite* cortical centre, and only by its most external lateral marginal part with the centre of the *same* side (fig. 613). If we imagine the surface of *one* retina to be projected upon the centres, then the most external margin of the first is connected with the centre of the *same* side, the inner margin of the retina with the inner area of the *opposite* centre, the upper margin with the anterior area, and the lower marginal part of the retina with the posterior area of the opposite side. The (shaded) middle of the centre corresponds to the position of direct vision of the retina of the *opposite* side (compare § 344).

Stimulation of the visual centre in the **dog** causes movements of the eyes towards the other side, sometimes with similar movements of the head and contraction of the pupils. If one eye be excised from new-born dogs, the opposite visual centre, after several months, is less developed (*Munk*). After **extirpation** of the visual centre in young dogs, the channels which connect it with the optic nerve undergo degeneration (*Monakow*) (§ 344).

In **monkeys**, the centre occupies the occipital lobe. Unilateral destruction causes temporary blindness of the halves of *both* retinæ, *i.e.*, hemianopia on the side of the injury. The visual centre in pigeons (fig. 609, IV, where 1 is placed) lies somewhat behind and internal to the highest curvature of the hemispheres (*M'Kendrick*, *Ferrier*, *Muschold*). The visual centre in the frog lies in the optic lobe (*Blaschko*).

[The **visual path** is along the optic nerve to the chiasma, where the fibres from the nasal half of each retina cross to the optic tract, some of the fibres perhaps becoming connected with the **external corpora geniculata**, and some with the **pulvinar** of the optic thalamus and **anterior corpora quadrigemina**, while the great mass sweeps backwards to the occipital lobes as the **optic expansion** or radiation of Gratiolet. Fibres arise in and pass from the optic thalamus through the internal capsule (p. 886) to the occipital lobe. Destruction of this path behind the chiasma causes **hemiopia** or **hemianopia**, and certain diseases of the occipital cortex cause a similar result. Perhaps, however, there is another centre in the angular gyrus (and supra-marginal lobe), for in cases of word-blindness disease has been found in these regions. Sometimes flashes of light or the appearance of a ball of fire form the aura in epilepsy, and Hughlings Jackson thinks that discharging lesions of the right occipital lobe cause coloured vision more frequently than those of the left.]

[Removal of the eyeball and section of the optic nerve result in degeneration of the optic tract, for if the eyeballs be removed in a young animal not only is there this centripetal degeneration but the external geniculate body, the pulvinar and

anterior corpora quadrigemina do not undergo complete development. The **trophic centre** for the fibres of the optic tract is in the nerve-cells of the **retina**, which, as its development shows, is really a part of the cerebral cortex greatly modified.

[It is stated that in new-born animals destruction of the temporal region results in imperfect development of the internal geniculate body and part of the posterior corpus quadrigeminum. Destruction of the internal ear leads to partial atrophy of the fillet. On these grounds it has been suggested, but not proved, that auditory impulses pass along the cochlear branch of the auditory nerve to the opposite auditory nucleus, thence into part of the fillet, from the latter into the posterior corpus quadrigeminum and internal geniculate body, and thence into the temporal region.

2. **The centre for hearing**, or "**auditory area**," lies in the **dog**, according to Ferrier, in the region of the second primary convolution at *f, f, f* (fig. 609, II), while in the **monkey** and **man** it is in the first temporal or temporo-sphenoidal gyrus (Ferrier's centre, No. 14). Munk locates it in the same region. According to Munk, destruction of the entire region causes deafness of the *opposite* ear, while destruction of the middle shaded part alone causes "**psychical deafness**" ("*Seelentaubheit*"). Electrical irritation of the upper two-thirds of the superior temporal convolution is followed by a reaction which closely resembles that produced by a sudden fright, or that produced by a sudden unexpected noise. [There is a quick retraction of the opposite ear, *i.e.*, "pricking" of the ear as if toward the supposed origin of the sound, combined generally with turning of the head and eyes to that side, and dilatation of the pupil.] Ferrier locates the centre for hearing in the monkey in the *superior temporo-sphenoidal convolution*, and he finds that, when the centres on both sides are *extirpated*, the animal is absolutely deaf; it takes no cognisance of a pistol fired in its neighbourhood. [From his experiments on monkeys, Schäfer denies absolutely the conclusions of the above-named experiments. Schäfer points out that it is not difficult to substantiate hearing in monkeys; it is difficult to substantiate deafness, for quite normal monkeys will often fail to pay the least attention to loud sounds. In six monkeys, Schäfer asserts that after more or less complete destruction of the superior temporal gyrus on both sides, hearing was not perceptibly affected. In one case both temporal lobes were completely removed without any permanent diminution in the acuteness of hearing. These results are opposed to the ordinary clinical teaching on this subject.] In **man**, injuries to the first and second temporo-sphenoidal convolutions on one side do not appear to cause complete deafness of one ear, as it seems that the sense of hearing for each ear is perhaps represented on both sides. Bilateral lesions of these convolutions in man cause complete deafness. Disease of these two convolutions is associated with **word-deafness** (p. 880). Wernicke cites the case of a person first affected with word-deafness, who afterwards became completely deaf; and after death a bilateral lesion was found in the first temporo-sphenoidal convolution. These convolutions are supplied with blood by the middle cerebral or Sylvian artery.

[The **auditory paths** are from the auditory nuclei in the medulla oblongata through the pons, where they perhaps cross into the tegmentum, thence into the "sensory crossway," and onwards to the auditory centre.]

[**Auditory Auræ.**—Equally important with these effects of disease are the sensory impressions, or "**auræ**," which sometimes usher in an attack of epilepsy; sometimes these auræ consist of sounds or noises, and in these cases the seat of the disease is often in the first temporo-sphenoidal convolution.]

[3. **The olfactory centre** has not been so definitely located as some of the others. There is strong presumptive evidence that it is situated in the hippocampal region of the temporal lobe, at its lower extremity. This view is strengthened by the anatomical relations of this region to the olfactory tract and anterior

commissure (*Ferrier*). M'Lane Hamilton has recorded a case of epilepsy ushered in by an aura of a disagreeable odour, in which there was atrophy of the grey matter of the right uncinate gyrus.]

[**Olfactory Path.**—Although the outer root of the olfactory tract runs direct to the uncinate gyrus, in *hemianæsthesia* resulting from injury to the "sensory crossway," smell is lost on the opposite side, while it is lost on the same side when the uncinate gyrus is involved. It may be that the impulses go first to their own side, and cross afterwards.]

[4. We do not know the **centre for taste**, and even the course of the nerve of taste is disputed. Ferrier places it close to that of smell.]

On stimulating the subiculum in monkeys, dogs, cats, and rabbits, he observed peculiar movements of the lips and partial closure of the nostrils on the same side (§ 365). In man, subjective olfactory and gustatory perceptions are regarded as irritative phenomena, while loss of these sensory activities, often complicated with other cerebral phenomena, is regarded as a symptom of their paralysis.

[The **gustatory path** crosses in the posterior part of the posterior segment of the internal capsule. While Gowers admits that the chorda tympani is the nerve of taste for the anterior two-thirds of the tongue, he thinks that it reaches the facial nerve from the spheno-palatine ganglion through the Vidian nerve. He denies that the glosso-pharyngeal is concerned in taste, and "he believes that taste impressions reach the brain solely by the roots of the 5th nerve." He admits that the nerves of taste to the back part of the tongue may be *distributed* with the glosso-pharyngeal, reaching them through the otic ganglion by the small superficial petrosal and tympanic plexus.]

[5. Ferrier places the **centre for tactile** sensation in the **hippocampal region**, close to the distribution of part of the posterior cerebral artery; so far this has not been confirmed. The centre for the sensation of **pain** has not been defined; probably it is very diffuse. **The limbic lobe**, according to Broca, includes the **hippocampal convolution** and the **gyrus fornicatus**. Ferrier found that removal of the hippocampal region resulted in a diminution of the sensibility of the opposite side of the body. Horsley and Schäfer observed only a temporary hemianæsthesia, but they found that an extensive lesion of the **gyrus fornicatus** was followed by hemianæsthesia, more or less marked and persistent, so that **cutaneous sensibility** has been referred to this convolution (fig. 607). From their experiments these observers conclude that the limbic lobe "is largely if not exclusively, concerned in the appreciation of sensations, painful and tactile."]

6. Munk is of opinion that the surface of the cerebrum in the region of the motor centres acts at the same time as "**sensory areas**" ("*Fühlsphäre*"), *i.e.*, they serve as centres for the *tactile* and *muscular* sensations and those of the innervation of the opposite side. He asserts that after injury to these regions the corresponding functions are affected.

According to Bechterew, the centres for the perception of tactile impressions, those of innervation, of the muscular sense, and painful impressions are placed in the neighbourhood of the motor areas (dog); the first immediately behind and external to the motor areas, the others in the region close to the origin of the Sylvian fissure. (See also p. 883.)

Goltz, who first accurately described the disturbances of vision following upon injuries to the cortex in dogs, is opposed to the view of sensory localisation. He believes that each eye is connected with both hemispheres. He asserts that the disturbance of vision, after injury to the brain, consists merely in a diminished colour- and space-sense. The recovery of the visual perception of one eye after injury of one side of the cortex cerebri, he explains by supposing that this injury merely causes a temporary inhibition of the visual activity in the opposite eye, which disappears at a later period. Instead of psychical blindness and deafness he speaks of a "cerebro-optical" and "cerebro-acoustical weakness."

377. **THERMAL CORTICAL CENTRES.**—Eulenburg and Landois discovered an area on the cortex cerebri, whose stimulation produced an undoubted effect upon the temperature and condition of the blood-vessels of the opposite extremities. This region (fig. 609, I, *t*) generally embraces the area in which, at the same time, the motor centres for the flexors and rotators of the fore limb (3), and for the muscles of the hind limb (4) are placed. The areas for the anterior and posterior limbs are placed apart, that for the anterior limb lies somewhat more anteriorly, close to the lateral end of the crucial sulcus. **Destruction** of this region causes increase of the temperature of the opposite extremities; the temperature may vary considerably (1°·5 to 2°, and even rising to 13° C.). This result has been confirmed by Hitzig, Bechterew, Wood, and others. This rise of the temperature is usually present for a considerable time after the injury,

although it may undergo variations. Sometimes it may last three months, in other cases it gradually reaches the normal in two or three days. In well-marked cases there is a diminution of the resistance of the wall of the femoral artery to pressure, and the pulse-curve is not so high (*Reinke*). Local electrical **stimulation** of the area causes a slight temporary cooling of the opposite extremities, which may be detected by the thermo-electric method. Stimulation by means of common salt acts in the same way, but in this case the phenomena of destruction of the centre soon appear. As yet, it has not been proved that there is a similar area for each half of the head. The cerebro-epileptic attacks (§ 375) increase the bodily temperature partly owing to the increased production of heat by the muscles (§ 302), partly owing to diminished radiation of heat through the cutaneous vessels, in consequence of stimulation of the thermal cortical nerves. The experiments led to no definite results when performed on rabbits. According to Wood, destruction of these centres occasions an increased production of heat that can be measured by calorimetric methods, while stimulation causes the opposite result.

These experiments explain how psychical stimulation of the cerebrum may have an effect upon the diameter of the blood-vessels and on the temperature, as evidenced by sudden paleness and congestion (§ 378, III.).

[**Heat Production.**—Injury to the fore-brain has no effect on the temperature. If the brain of a rabbit be punctured through the large fontanelle, and the stylette be forced through the grey matter on the surface, white matter, and the median portion of the corpus striatum right to the base of the brain, there is a rapid rise of the temperature, which may last several days. Injury to the grey cortex does not affect the temperature. After puncture of the corpus striatum, the highest temperature is reached only after twenty-four to seventy hours, but when the puncture reaches the base of the brain this result occurs in two to four hours. Electrical stimulation of these areas causes the same effect on the temperature. Direct injury to certain parts of the brain is followed by a rise of the temperature—or fever. See also p. 406 for further evidence of the existence of thermal centres. There is at the same time an increase of the O taken in, the CO_2 given off, and a decided increase of the N given off, indicating an increase in the proteid metabolism, which points to an increased production of heat (*Aronsohn and Sachs*, *Richet*, *Wood*).]

General and Theoretical.—Goltz's View.—Goltz uses a different method to remove the cortex cerebri—he makes an opening in the skull of a dog, and by means of a **stream of water** washes away the desired amount of brain-matter. He describes, first of all, **inhibitory phenomena**, which are **temporary** and due to a temporary suppression of the activity of the nervous apparatus, which, however, is not injured anatomically ; this may be explained in the same way as the suppression of reflexes by strong stimulation of sensory nerves (§ 361, 3). In addition, there are the **permanent phenomena**, due to the disappearance of the activity of the nervous apparatus, which is removed by the operation. A dog, with a large mass of its cerebral cortex removed, may be compared to an eating, complex, reflex machine. It behaves like an intensely stupid dog, walks slowly, with its head hanging down ; its cutaneous sensibility is diminished in all its qualities—it is less sensitive to pressure on the skin ; it takes less cognisance of variations of temperature, and does not comprehend how to feel ; it can with difficulty accommodate itself to the outer world, especially with regard to seeking out and taking its food. On the other hand, there is no paralysis of its muscles. The dog still sees, but it does not understand what it does see ; it looks like a somnambulist, who avoids obstacles without obtaining a clear perception of their nature. It hears, as it can be wakened from sleep by a call, but it hears like a person just wakened from a deep sleep by a voice—such a person does not at once obtain a distinct perception of the sound. The same is the case with the other senses. It howls from hunger, and eats until its stomach is filled ; it manifests no symptoms of sexual excitement.

Goltz supposes that every part of the brain is concerned in the functions of willing, feeling, perception, and thinking. Every section is, independently of the others, connected by conducting paths with all the voluntary muscles, and, on the other hand, with all the sensory nerves of the body. He regards it as possible that the individual lobes have different functions.

After removal of the anterior or **frontal convolutions** and the motor areas, there is at first unilateral motor and sensory paralysis and affection of vision. After some months, there remains only the loss of the muscular sense. If the operation be bilateral, the phenomena are more marked ; there are innumerable purposeless associated movements, and the dogs become vicious. Marked and permanent disturbance in the capacity to utilise the impressions from the sense-organs is not a necessary consequence of removal of the frontal convolutions.

Removal of the **occipital lobes** interferes most with vision. Bilateral removal makes the

animal almost blind. The dog remains obedient and lively. There is no disturbance of motion or of the muscular sense.

Inhibitory Phenomena.—Injury to the brain also causes inhibitory phenomena, such as the disturbances of motion, the complete hemiplegia which is frequently observed after large unilateral injuries of the cortex cerebri; these are regarded by Goltz as inhibitory phenomena, due to the injury acting on lower infra-cortical centres, whose action inhibits movement, but these movements are recovered as soon as the inhibitory action ceases.

Other Effects of Cortical Stimulation.—Some observers noticed variations of the **blood-pressure** and a change in the number of heart-beats after stimulation of the cortex cerebri, *e.g.*, after electrical stimulation of the motor areas for the extremities (*Bochefontaine*). Balogh observed acceleration of the **pulse**, on stimulating several points on the cortex cerebri of a dog, and from one point slowing of the pulse. Eckhard stimulated the surface of the brain in rabbits, and, as a rule, he observed that, as long as single crossed movements occurred in the anterior extremities, there was no effect upon the heart, but that the heart became affected as soon as other movements occurred. This consists in slow, strong pulse-beats, with occasional weaker beats, while at the same time the blood-pressure is slightly increased (*Bochefontaine*). If the vagi be divided beforehand, the effect upon the pulse disappears, while the increase of the blood-pressure remains. That psychical processes affect the action of the heart was known to Homer and Chrysipp. Bochefontaine and Lépine, on stimulating several points, especially in the neighbourhood of the sulcus cruciatus in the dog, observed increased secretion of **saliva**, slowing of the movements of the stomach, peristalsis of the intestine, contraction of the spleen, of the uterus, of the bladder, and increased respirations. Bufalini, on stimulating those parts of the cortex which cause movements of the jaw, observed secretion of gastric juice with increase of the temperature of the stomach. Schiff, Brown-Séquard, Ebstein, Klosterhalfen, and others have observed that injury to the pons, corpus striatum, thalamus, cerebral peduncle, and medulla oblongata often causes hyperæmia and **hæmorrhage** into the lung (according to Brown-Séquard, especially after injury to one side of the pons, which affects the opposite lung), under the pleura, in the stomach, intestine, and kidneys. Gastric hæmorrhage is common after injury to the pons just where the cerebral peduncles join it. Similar phenomena have been observed in man after apoplexy or cerebral hæmorrhage.

378. TOPOGRAPHY OF THE CORTEX CEREBRI.—A short *resumé* of the arrangement of convolutions, according to Ecker, is given in § 375.

I. The cortical **motor areas** for the face and the limbs are grouped around the

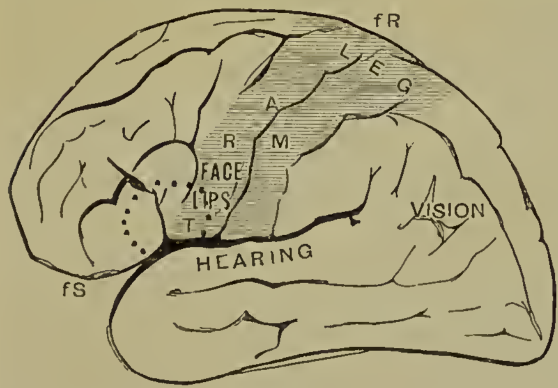


Fig. 614.

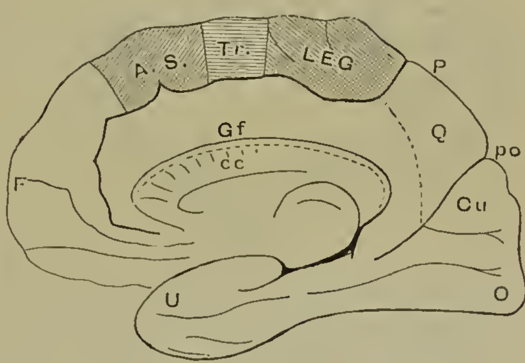


Fig. 615.

Fig. 614.—Motor areas in man, shaded—outer surface of the left side of human brain. Dotted area, the aphasic region (modified from Gowers). Fig. 615.—Inner surface of right hemisphere. *A.S.*, area governing the movements of the arm and shoulder; *Tr*, of the trunk; LEG, those of the leg; *Gf*, gyrus fornicatus; *CC*, corpus callosum; *U*, uncinate gyrus; *O*, occipital lobe.

fissure of Rolando, including the ascending frontal, ascending parietal, and part of the parietal lobule on the outer convex surface of the cerebrum (fig. 614). The centre for the **face** occupies the lowest third of the ascending frontal convolution, and reaches also to the lowest fifth of the ascending parietal. The **arm** centre occupies the middle third of the ascending frontal and middle three-fifths of the ascending parietal convolutions, while the **leg** centre lies at the upper end of the sulcus and extends backwards into the parietal lobule (and perhaps on to the

superior frontal convolution) (fig. 614). The **leg** centre is continued over on to the paracentral lobule, opposite the upper end of the fissure of Rolando, in the marginal convolution on the mesial aspect of the hemisphere (fig. 616), where the centres for the muscles of the trunk also exist (p. 864). The centre for **speech** is in the posterior part of the third left frontal convolution (fig. 614).

Blood Supply.—These convolutions are supplied with blood from 4 to 5 branches of the Sylvian artery, which may sometimes be plugged with an embolon. When a clot lodges in this artery, the branches to the basal ganglia may remain pervious, whilst the cortical branches may be plugged (*Duret*, *Heubner*) (§ 381).

[**Hemiplegia** consists of motor paralysis of one-half of the body, although, as a rule, all the muscles are not paralysed to the same extent; sometimes there may be complete paralysis, *i.e.*, they are entirely removed from voluntary control, while in others there is merely impaired voluntary control. It may be caused by affections of the cortical areas or by lesion of the motor tracts above the medulla, and the paralysis is always on the side opposite to the lesion, owing to the decussation of the motor paths in the medulla. If the case be a severe one, we have what Charcot terms *hemiplegie centrale vulgaire*, or "complete hemiplegia," due to lesion of the cortical centres for the face, arm, and leg. While the arm and leg are completely paralysed, the lower part of the face is more affected than the upper half, which is usually not much affected. All those movements under voluntary control, and especially those that have been learned, are abolished, whilst the associated and bilateral movements, which even animals can execute immediately after birth, remain more or less unaffected. Hence, the hand is more paralysed than the arm; this, again, than the leg; the lower facial branches more than the upper; the nerves of the trunk scarcely at all (*Ferrier*). When an extraordinary effort is made, it will be found that there is some impairment of the power of the muscles of mastication and respiration, although the muscles on opposite sides act together (*Gowers*). The trunk-muscles, as a rule, are but slightly affected, or not

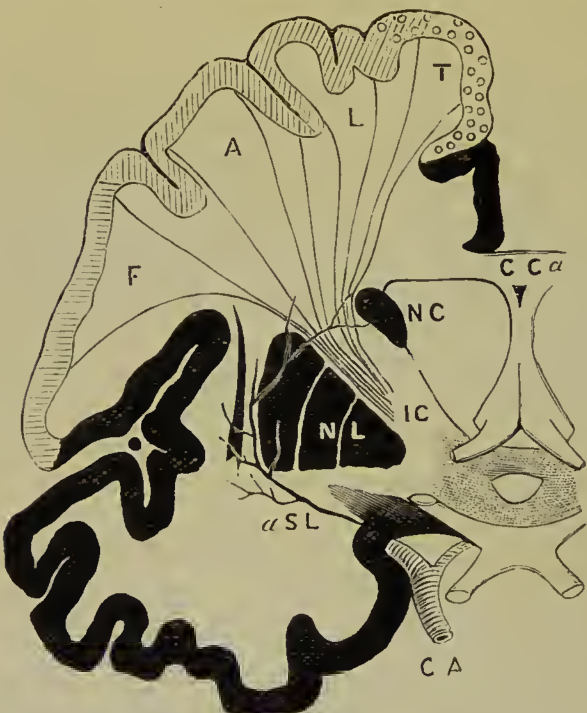


Fig. 616.

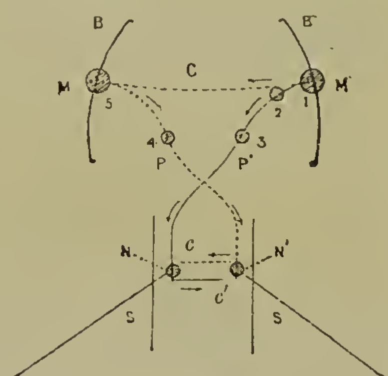


Fig. 617.

Fig. 616.—Transverse section of a cerebral hemisphere. CC*a*, corpus callosum; NC, caudate nucleus; NL, lenticular nucleus; IC, internal capsule; CA, internal carotid artery; *a*SL, lenticulo-striate artery; ("Artery of hæmorrhage"); F, A, L, T, position of motor areas governing the movements of the face, arm, leg, and trunk muscles of the opposite side (*Horsley*). Fig. 617.—Scheme of the innervation of bilaterally associated muscles (*Ross*).

at all, as their centre is elsewhere. There may be alterations of sensibility and of the reflexes.]

[Conduction through the whole of the pyramidal fibres coming from one hemisphere may be interrupted, and yet all the muscles on the opposite side of the body are not paralysed. The muscles which are comparatively unaffected are those associated in their action with the muscles of the opposite side, *e.g.*, the respiratory muscles. Broadbent assumes that such muscles have a bilateral representation in the motor areas. Suppose in fig. 617, B, B′, to represent the cerebral cortex ; M,M, motor centres in it ; N,N′, nerve nuclei in the spinal cord or medulla oblongata ; P,P′, the pyramidal tracts passing to spinal nuclei N, N′; *m,m′*, nerves proceeding from the last. 1, 2, 3, 4, 5, represent different lesions. In the case of muscles on opposite sides of the body, which act independently, *e.g.*, those of the hand, this is all the mechanism, but in bilaterally associated muscles there is another mechanism, viz., commissural fibres between the nerve nuclei, the one *c* conducting from right to left, and *c′* from left to right. When there is an injury at 1 or 3, impulses can still pass from the uninjured side M to N′ and through *c′* to the muscles *m, m′*. In this way both muscles receive motor impulses from one hemisphere (*Ross*).]

Conjugate deviation of the eyes, with rotation of the head, is frequently present in the early period of hemiplegia, although it usually disappears. When a person turns his head to one side, there is an associated movement of certain of the ocular muscles with those of the neck. The head and eyes are usually turned to the side of the lesion ; this is termed "conjugate deviation," so that the power of voluntarily moving the eyes and head to the paralysed side is temporarily lost. The unopposed muscles rotate the head and eyes to the sound side. If the lesion be in the posterior part of the pons, the deviation is to the paralysed side (*Prévost*). [Such movements have been obtained by stimulating the angular gyrus, and the posterior extremity of the middle frontal convolution.]

[**Subsequent Effects.**—If there be a hæmorrhage, say into these motor regions, or from the lenticulo-striate artery, so as to compress the pyramidal fibres in the knee and anterior two-thirds of the posterior segment of the internal capsule, then there is usually tonic or persistent contraction of the muscles affected. These tonic spasms may accompany the hæmorrhage, or come on a few days after it, and set up the condition of **early rigidity**. The contraction or spasm—if any—accompanying the hæmorrhage, is due to direct irritation of the pyramidal fibres, while that which comes on a few days later, and usually lasts a few weeks, is also due to irritation of these fibres, probably produced by inflammatory action in and around the seat of the lesion. The affected limb is stiff and resists passive movement. After a few weeks, **late rigidity** sets in and is persistent, and it is characterised by structural changes in the pyramidal paths which lead to other results. There is **secondary descending degeneration** in the pyramidal tracts, which causes "**contracture**" in the paralysed limbs, while at the same time the deep or tendinous and periosteal reflexes (ankle-clonus, rectus-clonus, and the deep reflexes of the arm-tendons) are exaggerated. The spastic rigidity is usually more marked in the arm than in the leg, and it generally affects the flexors more than the extensors, so that the upper arm is drawn close to the trunk, the elbow, arm, and fingers flexed ; in the leg, the extensors of the leg overcome the peronei. Hitzig has pointed out that the contracture is less during sleep, and after rest. The muscles at first can be stretched by sustained pressure, but after months or years structural changes occur in the muscles, ligaments, and tendons, and the limbs assume a permanent and characteristic attitude.]

In hemiplegic persons the power of the unparalysed side is sometimes diminished, which is not sufficiently explained by the fact that some bundles of the pyramidal tracts remain on the *same* side (*Brown Séquard, Charcot*).

[**Acquired Movements.**—Some movements performed by man are learned only after much practice, and are only completely brought under the influence of the will after a time, such as the movements of the hand in learning a trade. Such movements are reacquired only very slowly, or not at all, after injury to the motor areas in which they are represented. Those movements, however, which the body performs without previous training, such as the associated movements of the eyeballs, the face, and some of those of the legs, are rapidly recovered after such an injury, or they suffer but little, if at all. Thus, the facial muscles seem never to be so completely paralysed after a lesion of the facial cortical centre, as in affections of the trunk of the facial nerve ; the eye especially can be closed. Sucking movements have been observed in hemicephalous fœtuses.]

Degeneration of the Pyramidal Tracts.—After destruction of the cortical motor areas, descending degeneration of the cortico-motor paths, or "*pyramidal tracts*," takes place (§ 365). Degenerative changes have been found to occur within the white matter under the cortex in the anterior two-thirds of the posterior segment of the internal capsule, [in the middle third of the crusta (figs. 618, *, 619, L], pons, in the anterior pyramids of the medulla oblongata (fig. 618), and thence

they have been traced into the pyramidal paths (direct and crossed) of the spinal cord (*Charcot, Singer*). It is evident that lesions of these tracts at any part of their course must have the same result, viz., to produce hemiplegia. (For the subsequent effects, see p. 780). In a case of congenital absence of the left fore-arm, Edinger found that the right central convolutions were less developed.

[The descending degeneration in the pyramidal tracts shows that their **trophic centre** lies in the cells of the motor part of the cortex. The course of the fibres from the motor areas and their relative position in the internal capsule may be traced by the course of the descending degeneration following upon removal of a particular cortical motor area. France has shown that removal either of the marginal or forniecate gyrus is followed by descending degeneration of the opposite crossed pyramidal tract traceable to the lower lumbar region.]

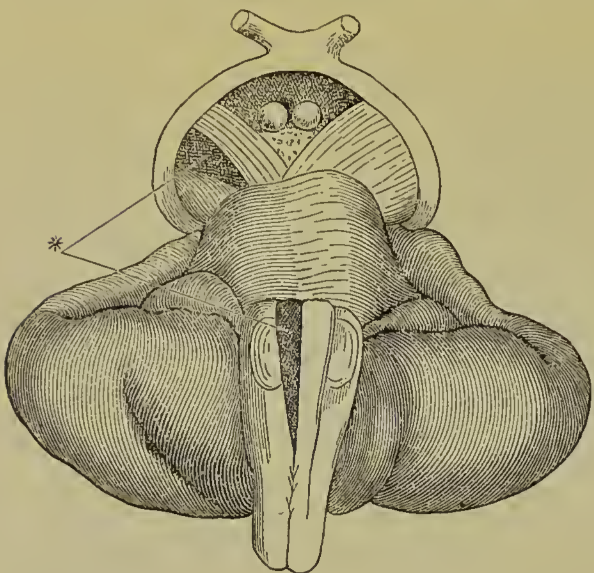


Fig. 618.

Fig. 619.

Fig. 618.—Secondary descending degeneration in middle third of right crus and medulla, after destruction of the cortical motor centres on the right side. Fig. 619.—Horizontal section of the cerebral peduncle in secondary degeneration of the pyramidal tracts, where the lesion was limited to the middle third of the posterior segment of the internal capsule. F, healthy crusta ; L, locus niger ; P, internal third of the crusta on the diseased side ; D, secondary degeneration in the middle third of the crusta ; CQ, corpora quadrigemina with the iter below them.

It is doubtful if the **muscular sense** is represented in the motor areas ; Nothnagel supposes it to be located in the temporal parietal lobes. It is to be noted, however, that in man there may be general loss of the muscular sense or of motor representations, and, on the other hand, a pure motor paralysis without loss of the former.

Ataxic motor conditions, similar to those that occur in animals (p. 755), take place in man, and are known as *cerebral ataxia*.

The **position of the centres** is given at p. 862.

[But we may have **localised lesions** affecting one or more of the cortical motor areas ; these are called **monoplegiæ**. Cases in man are now sufficiently numerous to permit of accurate diagnosis.] **Crural monoplegia** [rare lesions recorded in the convolutions at the upper end of the fissure of Rolando, and the continuation of this area on to the paracentral lobule of the marginal convolution], **brachio-crural**, more common, in the upper and middle thirds of the ascending frontal and ascending parietal convolutions—**brachial, brachio-facial**—**facial**, the last in the lowest part of the central convolutions.

Paralysis of the muscles of the neck and throat indicates a lesion of the central convolutions, and so does paralysis of the muscles of the eye. Lesions of the cortex always cause simultaneous movements of the head and eyeballs.

Irritation of the Motor Centres.—If the motor centres are irritated by pathological processes, such as hyperæmia, or inflammation in a syphilitic diathesis—more rarely by tumours, tubercle, cysts, cicatrices, fragments of bone—there arise spasmodic movements in the corresponding muscle-groups. This condition of a sudden discharge of the grey matter resulting in local spasms is called "**Jacksonian, or cerebral epilepsy.**"

[Convulsions and spasms may be discharged from motor cortical lesions, and these, whether they affect the general or localised areas, give rise to unilateral convolutions and **monospasm** respectively.]

Monospasm.—According to the seat of the spasm, it is called *facial, brachial, crural monospasm*, &c. Of course these spasms may affect several groups of muscles. Bartholow and Sciamanna have stimulated the exposed human brain successfully with electricity.

Cerebral Epilepsy.—Very powerful stimulation of *one* side may give rise to *bilateral* spasms, with loss of consciousness. In this case, impulses are conducted to the other hemisphere by commissural fibres (§ 379). [It is most readily produced in animals lower in the scale than monkeys (p. 862).]

Movements of the Eyeball.—Nothing definite is known regarding the centre in the cortex for voluntary *combined movements* of the eyeballs in man. In paralytic affections of the cortex and of the paths proceeding from it, we occasionally find both eyes with a lateral deviation. If the paralytic affection lies in one cerebral hemisphere, the **conjugate deviation** of the eyeballs is towards the sound side (§ 345). If it is situated in the conducting paths, after these have decussated, viz., in the pons, the eyes are turned towards the paralysed side (*Prévost*).

If the part be irritated so as to produce spasms in the opposite half of the body, of course the eyes are turned in the direction opposite to that in pure paralysis. Instead of the lateral deviation of the eyeballs already described, there is occasionally in cerebral paralysis merely a *weakening* of the lateral recti muscles, so that during rest the eyes are not yet turned towards the sound side, but they cannot be turned strongly towards the affected side (*Leichtenstern, Hunnius*). The centre for the levator palpebræ superioris appears to be placed in the angular gyrus (*Grasset, Landouzy*).

II. The Centre for Speech.—The investigations of Bouilland [1825], Dax [1836], Broca [1861], Kussmaul, Broadbent, and others have shown that the **third left frontal convolution** of the cerebrum (figs. 610, F3, and 614) is of essential importance for speech, while probably the island of Reil also is concerned. The island is deeply placed, and is seen on lifting up the overhanging part of the brain called the operculum, lying between the two branches of the Sylvian fissure (S). The motor centres for the organs of speech (lips, tongue) lie in this region, and here also the psychical processes in the act of speech are completed. In the great majority of mankind, the centre for speech is located in the *left* hemisphere. The fact that most men are *right-handed* also points to a finer construction of the motor apparatus for the upper extremity, which must also be located in the left hemisphere. Men, therefore, with pronounced *right-handedness* ("droitors") are evidently *left-brained* ("gauchers du cerveau"—*Broca*). By far the greater number of mankind are "*left-brained speakers*" (*Kussmaul*); still there are exceptions. As a matter of fact, cases have been observed of *left-handed* persons who lost their power of speech after a lesion of the *right* hemisphere (*Ogle*). Investigations on the brains of remarkable men have shown that in them the third frontal convolution is more extensive and more complex than in men of a lower mental calibre. In deaf-mutes it is very simple; microcephales and monkeys possess only a rudimentary third frontal (*Rüdinger*).

The **motor tract for speech** passes along the upper edge of the island of Reil, then into the substance of the hemispheres internal to the posterior edge of the knee of the internal capsule; from thence, through the crusta of the left cerebral peduncle into the left half of the pons, where it **crosses**, then into the medulla

oblongata, which is the place where all the motor nerves (trigeminus, facial, hypoglossal, vagus, and the respiratory nerves) concerned in speech arise. Total destruction of these paths, therefore, causes total aphasia; while partial destruction causes a greater or less disturbance of the mechanism of articulation, which has been called "**anarthria**" by Leyden and Wernicke.

Conditions for Speech.—Three activities are required for speech—(1) the normal movement of the vocal apparatus (tongue, lips, mouth, and respiratory apparatus); (2) a knowledge of the signs for objects and ideas (oral, written and imitative or mimetic signs); (3) the correct union of both.

Aphasia (ἀ priv. and φάσις speech).—Injury of the speech-centre causes either a loss or more or less considerable disturbance of the power of speech. The loss of the power of speech is called "*aphasia.*" [Aphasia, as usually understood, means the partial or complete loss of the power of articulate speech from cerebral causes. The person is speechless, but not necessarily absolutely wordless.]

The following **forms** of aphasia may be distinguished:—

1. **Ataxic aphasia** (or the oro-lingual hemiparesis of Ferrier), *i.e.*, the loss of speech owing to inability to execute the various movements of the mouth necessary for speech. Whenever such a person attempts to speak, he merely executes inco-ordinated grimaces and utters inarticulate sounds. [The muscles concerned in articulation, however, are not paralysed, but there is an absence of co-ordination of these muscles due to disease of the cortical centre.] Hence, the patient cannot repeat what is said to him. Nevertheless, the *psychical* processes necessary for speech are completely retained, and all words are remembered; and hence, these persons can still give expression to their thoughts graphically or by *writing.* If, however, the finely adjusted movements necessary for writing are lost, owing to an affection of the centre for the hand, then there arises at the same time the condition of **agraphia**, or inability to execute those movements necessary for writing. Such a person, when he desires to express his ideas in writing, only succeeds in making a few unintelligible scrawls on the paper. Occasionally such patients suffer from loss of the power of imitation or the execution of particular movements of the limbs and body constituting *pantomime* speech or **amimia** (*Kussmaul*).

2. **Amnesic Aphasia** or Loss of the Memory of Words.—Should the patient, however, hear the word, its significance recurs to him. The movements necessary for speech remain intact; hence, such a patient can at once repeat or write down what is said to him. Sometimes only certain kinds of words are forgotten, or it may be even only parts of certain words, so that only part of these words is spoken. [Nouns and proper names usually go first.] Cases of amnesic aphasia, or the mixed ataxic-amnesic form of disturbance of speech, point to a lesion of the third frontal convolution and of the island of Reil on the *left* side. Another form of amnesic aphasia consists in this, that the words remain in one's memory but do not come when they are wanted, *i.e.*, the association between the idea and the proper word to give expression to it is inhibited (*Kussmaul*). It is common for old people to forget the names of persons or proper names; indeed, such a phenomenon is common within physiological limits, and it may ultimately pass into the pathological condition of **amnesia senilis.** Amongst the disturbances of speech of *cerebral* origin, Kussmaul reckons the following:—

3. **Paraphasia**, or the inability to connect rightly the ideas with the proper words to express these ideas, so that, instead of giving expression to the proper ideas, the sense may be inverted, or the form of words may be unintelligible. It is as if the person were continually making a "slip of the tongue."

4. **Agrammatism** and **ataxaphasia**, or the inability to form the words grammatically and to arrange them synthetically into sentences. Besides these, there is—

5. A pathological slow way of speaking (**bradyphasia**), or a pathological and stuttering way of reading (**tumultus sermonis**), both conditions being due to derangement of the cortex (*Kussmaul*). The disturbances of speech depending essentially upon affections of the *peripheral* nerves, or of the muscles of the organs of the voice and speech, are already referred to in §§ 319, 349, and 354.

[In **word-blindness**, the person cannot name a letter or a word, so that he cannot understand symbols, such as printed or written words, or it may be any familiar object, although he can see quite well, while he can speak fluently and write correctly.]

[In **word-deafness**, the person hears other sounds and is not deaf, but he does not hear words.]

[The study of aphasia in its various forms is simplified by a study of the mode of **acquisition of language** by a child. The child hears spoken words and obtains auditory memories of

impressions of these sounds (called by Lichtheim "**auditory word-representations**"), and this must form the starting-point of language, and by and by it begins to co-ordinate its muscles to produce sounds imitative of these. Thus we have two centres, one for "**auditory images**" (fig. 620, A), and the other for "**motor images**" (fig. 620, M), and these two must be connected, thus establishing a reflex arc. There is a receptive and an emissive department as represented in the scheme. We must assume the existence of a higher centre (B), "in which concepts are elaborated," where these sounds become intelligible. Volitional language requires a connection between B and M, as well as between A and M. But we have also **reading** and **writing**. Suppose O to represent a centre for visual impressions (printed words or writing): these we can understand through the connection between such visual impressions and auditory impressions, whereby a path is established through OA (fig. 621). In reading aloud, however, the orolingual muscles must be co-ordinated, so we have the path OAM opened up. In writing, or copying written characters, the movements of the hand are special, and perhaps require a special centre, or at least a special arrangement of the channels for impulses in the centre; the movements are learned under the guidance of ocular impressions, so we connect O and E, E being the centre guiding the movements in writing. As to volitional writing, the impulse passes through M—but does it pass directly to E, or indirectly through A? Lichtheim assumes that it goes direct from M to E. It is evident that there are seven channels which may be interrupted, each one giving rise to a different form of aphasia (1 to 7).]

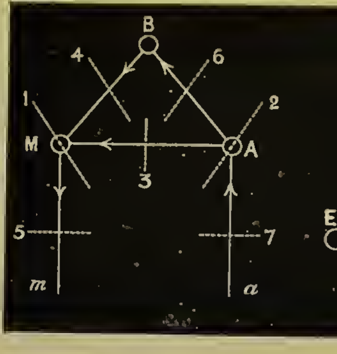


Fig. 620.

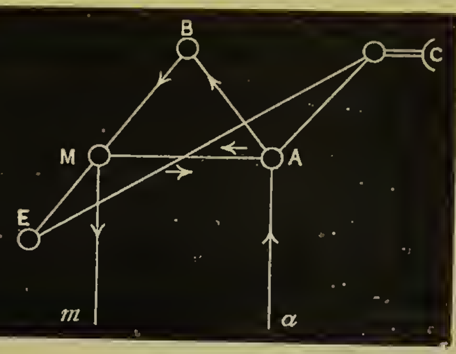


Fig. 621.

Figs. 620, 621.—Schemes of aphasia. A, centre for auditory images; M, for motor images; B, perception centre; Oc, eye; E, reading centre; 1 to 7, lesions (*Lichtheim*).

[Looked at from another point of view, either the ingoing (a) or outgoing (m) channels or centres, or the commissural fibres between both, may be affected. If the motor centre is affected, we have Wernicke's "**motor aphasia**"; if the sensory, his "**sensory aphasia.**"]

[In the most common form, or **ataxic aphasia** (*Kussmaul*), which was that described by Broca, or the "motor aphasia" of Wernicke, the lesion is in fig. 620, in M, *i.e.*, in the motor, or what Ross calls the emissive department. In such a case, it is obvious that there will be **loss** of (1) volitional speech, (2) repetition of words, (3) reading aloud, (4) volitional writing, and (5) writing to dictation; while there will **exist** (a) understanding of spoken words, (b) also of written words, (c) and the faculty of copying. If the lesion be in A, we have the "**sensory aphasia**" of Wernicke, *i.e.*, in the acoustic word-centre; we find **loss of** (1) understanding of spoken language, (2) also of written language, (3) faculty of repeating words, (4) and of writing to dictation, (5) and of reading aloud; there will **exist** (a) the faculty of writing, (b) of copying words, and (c) of volitional speech, but the volitional speech is imperfect, the wrong word being often used, so that there is the condition of "**paraphasia.**" If the connection between A and M be destroyed, other results will follow, and such cases of "commissural" aphasia have been described by Wernicke. If the interruption be between B and M, we have a not uncommon variety of motor aphasia (4), where there is **loss of** (1) volitional speech, and (2) volitional writing, and there **exist** (a) understanding of spoken language, (b) of written language, (c) and the faculty of copying; but it differs from Broca's aphasia in that there also exists the faculty (d) of repeating words, (e) of writing to dictation, (f) and of reading aloud. If the lesion is in Mm (5), the symptoms will be those of Broca's aphasia, but there will exist (1) the faculty of volitional writing, and (2) of writing to dictation. Many examples of this occur where patients have lost the faculty of speaking, but can express their thoughts in writing. In lesions of the path AB (6), there will be **loss of** (1) understanding of spoken language, and (2) of written language, and there will **exist** (a) volitional speech (but it will be paraphasic), (b) volitional writing (but it will have the characters of paragraphia), (c) the faculty of repeating words, (d) reading aloud, (e) writing to dictation, and (f) power of copying words. The person will be quite unable to understand what he repeats, reads aloud, or copies.]

[Fig. 622 shows diagrammatically the conditions in motor and sensory aphasia. From the eye and ear centripetal fibres (v and a) ascend to terminate in the visual (V) and auditory centres (A), in the cortex, while afferent fibres (s, s′, s″), indicated by dotted lines, also pass from the articulations, muscles of the hand, and orbit to the cerebrum. The dotted lines on the surface of the cortex represent the association system of fibres which connects the centres with

each other. The centres for vocal (V) and written expression (W) are connected by centrifugal fibres, m and m', with the hand and larynx respectively (*Ross*).]

III. The thermal centre for the extremities is associated with the motor areas (§ 377). Injury or degeneration of these areas causes inequality of the temperature on both sides (*Bechterew*).

IV. The sensory regions are those areas in which conscious perceptions of the sensory impressions are accomplished. Perhaps they are the substratum of sensory perceptions, and of the memory of sensory impressions.

1. **The visual centre**, according to Munk, includes the occipital lobes (fig. 610, O^1, O^2, O^3), while, according to Ferrier, it also includes the angular gyrus. Huguenin observed, in a case of long-standing blindness, consecutive diminution of the occipital convolutions on both sides of the parieto-occipital fissure, while Giovanardi, in a case of congenital absence of the eyes, observed atrophy of the occipital lobes, which were separated by a deep furrow from the rest of the brain. Stimulation of the centre gives rise to the phenomena of light and colour. Injury causes disturbance of vision, especially hemiopia of the same side (§ 344—*Westphal*). When *one* centre is the seat of irritation, there is photopsia of the same halves of both eyes (*Charcot*). Stimulation of both centres causes the occurrence of the phenomena of light or colour, or visual hallucinations in the entire field of vision. Cases of injury to the brain, where the sensations of light and space are quite intact, and where the colour sense alone is abolished, seem to indicate that the colour sense centre must be specially localised in the visual centre (*Samelsohn*). After injury of certain parts, especially of the lower parietal lobe, "*psychical blindness*" may occur. A special form of this condition is known as "**word-blindness**" or **alexia** (Coecitas verbalis), which consists in this that the patient is no longer able to recognise ordinary written or printed characters (p. 880).

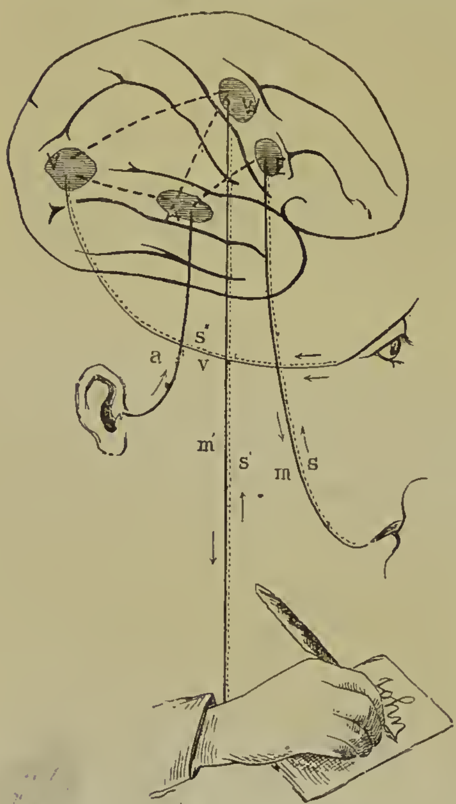


Fig. 622.
Scheme to illustrate aphasia.

Charcot records an interesting case of psychical blindness. After a violent paroxysm of rage, an intelligent man suddenly lost the memory of visual impressions; all objects (persons, streets, houses) which were well known to him appeared to be quite strange, so that he did not even recognise himself in a mirror. Visual perceptions were entirely absent from his dreams.

Clinical observations on **hemianopia** (§ 344) show that the field of vision of each eye is divided into a larger outer and a smaller inner portion, separated from each other by a vertical line passing through the macula lutea. Each right or left half of both visual fields is related to *one* hemisphere; both left halves are projected upon the left occipital lobes, and both right upon the right occipital lobes (fig. 613). Thus, in binocular vision, every picture (when not too small) must be seen in two halves; the left half by the left, the right half by the right hemisphere (*Wernicke*).

As a result of pathological stimulation of the visual centre, especially in the insane, visual spectres may be produced. Pick observed a case where the hallucinations were confined to the right eye. Celebrated examples of ocular spectra occurred in Cardanus, Swedenborg, Nicolais, J. Kerner, and Hölderlin.

After degeneration of the cortical centre the fibres which connect the occipital lobes with the

external geniculate body, the anterior corpora quadrigemina, pulvinar, these structures themselves, and the origin of the optic tract undergo degeneration (*v. Monakow*).

2. The **auditory centre** lies on both sides (crossed) in the temporo-sphenoidal lobes [according to Ferrier in the superior temporal convolution]; when it is completely removed, deafness results, while partial (left side) injury causes psychical deafness. [See p. 872 for contradictory results.] Amongst the phenomena caused by partial injury is *surditas verbalis* (**word-deafness**), which may occur alone or in conjunction with coecitas verbalis. Wernicke found in all cases of word-deafness softening of the first left temporo-sphenoidal convolution (p. 880). In left-handed persons the centre lies perhaps in the right temporo-sphenoidal lobes (*Westphal*).

Clinical.—We may refer word-blindness and word-deafness to the aphataxic group of diseases, in so far as they resemble the amnesic form. A person word-blind or word-deaf resembles one who in early youth has learned a foreign tongue, which he has completely forgotten at a later period. He hears or reads the words and written characters; he can even repeat or write the words, but he has completely lost the significance of the signs. While an amnesic aphasic person has only lost the key to open his vocal treasure, in a person who is word-blind or word-deaf even this is gone. From a case of recovery it is known that to the patient the words sound like a confused noise. Huguenin found atrophy of the temporo-sphenoidal lobes after long-continued deafness.

3. **Gustatory and Olfactory Centre.**—In the uncinate gyrus on the *inner* side of the temporo-sphenoidal lobe (especially on the inner side of that marked U in fig. 607), Ferrier locates the joint centres for smell and taste. These two centres do not seem to be distinct locally from each other.

4. **Tactile Areas** and **Cutaneous Sensibility.**—According to Tripier and others, all the *tactile* cerebral fields from different parts of the body coincide with the motor cortical centres for these parts (compare p. 873). [Schäfer and Horsley find that stimulation of the gyrus fornicatus gives rise to no muscular contractions, but its removal is followed by diminution in general and tactile sensibility of the opposite side of the body. See fig. 607, where this convolution is marked with the words "cutaneous sensation."]

Occasionally, in epileptics, strong stimulation of the sensory centres, as expressed in the excessive subjective sensations, accompanies the spasmodic attacks (compare § 393, 12). Such epileptiform hallucinations, however, occur without spasms, and are accompanied only by disturbances of consciousness of very short duration (*Berger*).

Course of the Sensory Paths.—The nerve-fibres which conduct impulses from the sensory organs to the sensory cortical centres pass through the *posterior third* of the *posterior limb of the internal capsule* between the optic thalamus and the lenticular nucleus (fig. 626, S). Hence, section of this part of the internal capsule causes **hemianæsthesia** of the opposite half of the body (*Charcot*). In such a case, sensory functions are abolished—only the viscera retaining their sensibility. There may also be loss of hearing, smell, and taste,—and hemiopia (*Bechterew*).

Pathological.—In cases where there is more or less injury or degeneration of these paths, there is a corresponding greater or less pronounced loss of the pressure and temperature sense, of the cutaneous and muscular sensibility, of taste, smell, and hearing. The eye is rarely quite blind, but the sharpness of vision is interfered with, the field of vision is narrowed, while the colour sense may be partially or completely lost. The eye on the same side may suffer to a slight extent.

V. Numerous cases of injury of the **anterior frontal region**, without interference with motor or sensory functions, have been collected by Charcot, Ferrier, and others. On the other hand, enfeeblement of the intelligence and idiocy are often observed in acquired or congenital defects of the prefrontal region. In highly intellectual men, Rüdinger found in addition a considerable development of the temporo-sphenoidal lobe. According to Flechsig, there is no doubt that the frontal lobes and the temporo-occipital zone are related to intellectual processes, more especially the "higher" of these.

Topography of the Brain.—The relations of the chief fissures and convolutions of the brain to the surface of the skull are given in fig. 610, the brain being represented after Ecker. [Turner

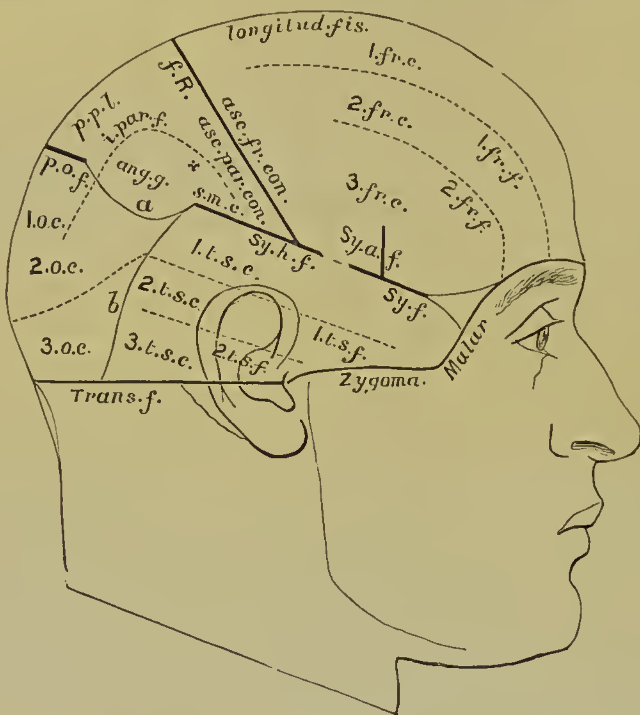


Fig. 623.

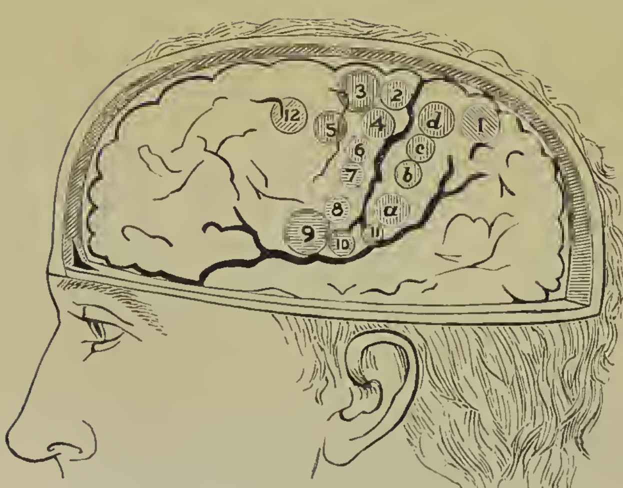


Fig. 624.

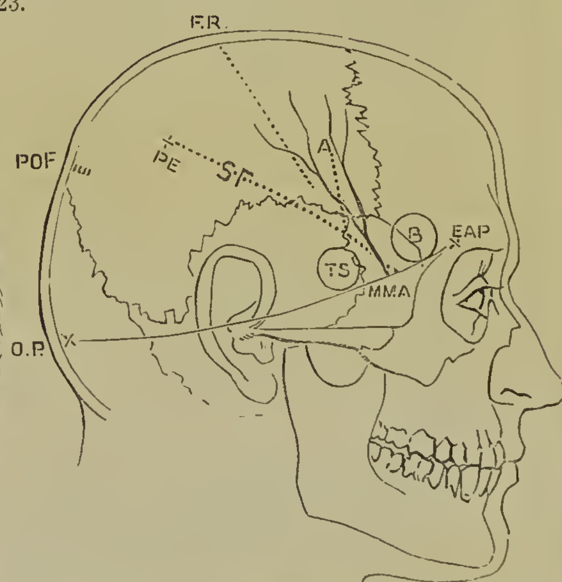


Fig. 625.

Fig. 623.—Relation of the fissures and convolutions to the surface of the scalp. +, most prominent part of the parietal eminence ; *a*, convex line bounding parietal lobe below; *b*, convex line bounding the temporo-sphenoidal lobe behind (*R. W. Reid*). Fig. 624.—The fissures of Rolando and Sylvius are marked as broad dark lines. The shaded circles mark approximately the motor areas. 1, lower extremity ; 2, 3, 4, 5, 6, and *a*, *b*, *c*, *d*, upper extremity ; 7, 8, 9, 10, 11, oro-lingual muscles (*A. W. Hare*). Fig. 625.—Head, skull, and cerebral fissures. OP, occipital protuberance ; EAP, external angular process ; SF, Sylvian fissure ; A, its ascending limb ; FR, fissure of Rolando ; PE, parietal eminence, MMA, middle meningeal artery; TS, tip of temporo-sphenoidal lobe ; B, Broca's convolution ; IF, inferior frontal sulcus ; POF, parieto-occipital fissure.

and others have given minute directions for finding the position of the different convolutions by reference to the sutures and other prominent parts of the skull. The annexed diagram by R. W. Reid shows the relation of the convolutions to certain fixed lines (fig. 623).]

[The position of the **fissure of Rolando**, where its upper end joins the great longitudinal fissure, is obtained by measuring on the scalp K in the middle line the distance between the glabella and the external occipital protuberance, or the inion, which in ordinary heads varies from 11 to 13 inches (fig. 625). Measured from before backwards, along this line, the distance from the glabella to the top of the fissure is 55·7 per cent. of the length of the whole line. The direction of the fissure is downwards and forwards, and the long axis of the fissure forms, with the average mesial line, an angle of 67°, the angle opening forwards. Its average length is $3\frac{3}{8}$ inches.]

[The **fissure of Sylvius** is found by drawing a line from the external angular process of the frontal bone backwards to the occipital protuberance, taking the nearest route between these two points. A point, $1\frac{1}{4}$ inch backwards from the angular process along this line, marks the origin of the fissure; while a straight line drawn to the centre of the parietal eminence marks the course of its posterior limb. The parieto-occipital fissure will be two inches behind the upper end of the Rolandic fissure (*A. W. Hare*).]

Corpus Callosum.—It is usually stated that the corpus callosum connects the convolutions of one side of the brain with those on the other, *i.e.*, that it is an interhemispherical commissure.

D. J. Hamilton, however, is of opinion that it is not an inter-hemispheric commissure, but is due to cortical fibres coming from the cortex cerebri to be connected with the basal ganglia of the opposite side.

Section of the corpus callosum in dogs, however, produces no obvious disturbance (*v. Korányi*). In man a case was described by Erb in which it was almost completely destroyed, yet there was no marked disturbance of motion, co-ordination, sensibility, the reflexes, intelligence, speech, or any marked impairment of the intelligence. The posterior part of the anterior commissure serves to connect the two gyri linguales (*Popoff*).

[379. **BASAL GANGLIA—MID BRAIN.**—By the term "**basal ganglia**" is meant the masses of grey matter constituting the corpus striatum and optic thalamus lying on the crus cerebri and at the base of the brain. Although they are grouped together, they are quite different in their origin, connections, and functions. The corpus striatum is developed in the wall of the cerebral vesicle, and comes to form the lateral wall of the lateral ventricles. It has few direct connections with the cortex. The optic thalamus is developed in the wall of the third ventricle, which it bounds laterally. It has connections with almost every part of the cortex cerebri above, and with the tegmentum of the crus cerebri. It is thus intercalated in the course of afferent impulses passing to the cortex through the tegmentum.]

[The **corpus striatum** consists of two parts, an intra-ventricular portion projecting into the lateral ventricle, the **caudate nucleus**, and an extra-ventricular portion, the **lenticular nucleus.** Between the head of the caudate nucleus internally and the lenticular nucleus externally, lies the anterior division or anterior limb of the internal capsule. The fibres which pass between these ganglia do not seem to form connections with them. The expanded head of the caudate nucleus is in front, and lies inside and around the front, of the lenticular nucleus, with which and the anterior perforated space it is continuous; it sweeps backwards into a tailed extremity, which nearly surrounds the lenticular nucleus like a loop. The **lenticular nucleus** is biconvex in a horizontal section, but triangular and subdivided into three divisions when seen in a vertical section (fig. 627). The older observations on the corpora striata in man may be dismissed, as a distinction was not drawn between injury to its two parts on the one hand and the internal capsule on the other.]

[The **caudate nucleus** and **lenticular nucleus** in their development are co-ordinate with the development of the cortex cerebri. **Electrical stimulation** of these ganglia causes general muscular contractions in the opposite half of the body, which are due to simultaneous stimulation of the neighbouring cortico-muscular

paths. The same result is obtained as if all the motor cortical centres were stimulated simultaneously. Beevor and Horsley regard the basal ganglia as inexcitable, at least they failed to get the slightest movement by exciting the sectional surfaces of either of these ganglia.]

Gliky did not observe movements on stimulating the corpus striatum in rabbits; it would seem that in these animals the motor paths do not traverse these ganglia, but merely pass alongside of them.

[**Lesions** of the lenticular nucleus or of the caudate nucleus do not seem to give rise to any permanent symptoms, provided the internal capsule be not injured.] Destruction of the internal capsule, however, causes paralysis of motion of sensibility, or both, on the opposite side of the body, according to the part of it which is injured. The corpus striatum is quite insensible to painful stimulation (*Longet*).

Pathological.—In **man**, a lesion, not too small, destroying the anterior part of the corpus striatum, is followed by permanent paralysis of the opposite side, provided the internal capsule is injured, but the paralysis gradually disappears if the lenticular and caudate nucleus only are affected (compare § 365). Sometimes there is dilatation of the blood-vessels in consequence of vaso-motor paralysis (§ 377) if the posterior part is injured (*Nothnagel*); redness and a slightly increased temperature of the paralysed extremities, at least for a certain time; swelling or œdema of the extremities; sweating; anomalies of the pulse detectable by the sphygmograph; decubitus acutus on the paralysed side; abnormalities of the nails, hair, skin; acute inflammation of joints, especially of the shoulder. Later, **contracture** or permanent contraction of the paralysed muscles takes place (*Huguenin, Charcot*). In some cases there is cutaneous anæsthesia, and occasionally enfeeblement of the sense-organs of the paralysed side, and both when the posterior third or sensory crossway of the posterior section of the internal capsule is affected. Usually, however, *hemiplegia* and *hemianæsthesia* occur together.

[**Optic Thalamus.**—It is developed in the wall of the vesicle of the third ventricle, and hence forms the lateral wall of this cavity. It is a mass of grey matter lying obliquely on and partly embedded in the crus. Its ventricular surface is covered with a thin layer of grey matter, and the whole thalamus consists of grey matter mixed with white matter. The nerve-cells are large and branched and frequently contain pigment. The posterior free cushion-like part is called the pulvinar, while the larger anterior part contains three nuclei known as the **inner** or **median nucleus**, the **lateral**, and **anterior nucleus.** Under the thalamus and dorsal to the tegmentum is the **sub-thalamic region** in which the tegmentum ends.]

[**Connections of the Optic Thalamus.**—This body is said to receive fibres from all parts of the cortex, while it is also connected with the tegmental system and with certain fibres of the optic tract.]

Functions of the Optic Thalamus.—Ferrier did not observe any movements on stimulating the optic thalami with electricity. As the pulvinar, or posterior extremity of the optic thalamus, is in part the origin of the optic nerve, and is also connected by fibres with the cortex cerebri, it is probably related to the sense of sight. Injury to its posterior third in man results in disturbance of vision (*Nothnagel*). Ferrier surmises that the sensory fibres pass through the optic thalami on their way to the cortex, so that when they are destroyed insensibility of the opposite half of the body is produced. Removal of the optic thalamus, or destruction of the part in the neighbourhood of the inspiratory centre in the wall of the third ventricle, influences the co-ordinated movements in the rabbit (*Christiani*).

We know very little definitely as to the functions of these organs. After injury to one thalamus, there has been observed enfeeblement or paralysis of the muscles of the opposite side, together with mouvements de manège; and sometimes hemianæsthesia of the opposite side, with or without affections of the motor areas, have been recorded. Extirpation of certain cortical areas (rabbit) is followed by atrophy of certain parts of the thalamus (*v. Monakow*).

Relation of basal ganglia to internal capsule.—The corpus striatum consists of an intra-ventricular part, the **caudate nucleus**, and an extra-ventricular part—

i.e., no part of this appears in the lateral ventricle—the **lenticular nucleus.** The **lenticular nucleus,** a mass of grey matter, consists of three parts, best seen in a vertical section (fig. 627, 1, 2, 3), with white matter between them, the **striæ**

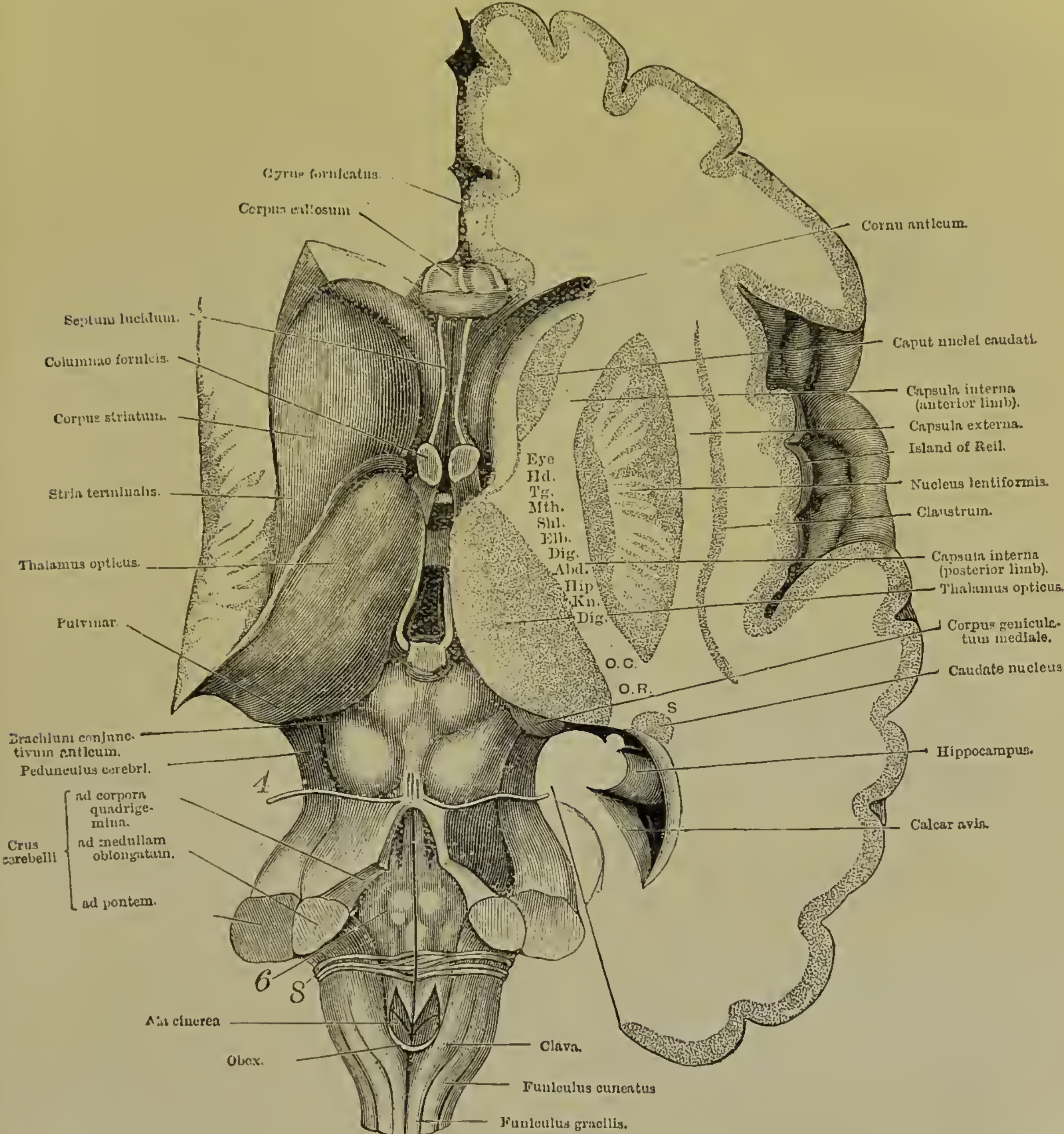


Fig. 626.

Human brain, with the hemispheres removed by a horizontal incision on the right side. 4, trochlear ; 8, acoustic nerve ; 6, origin of the abducens ; relative position of the pyramidal (motor) fibres of the eye, head (Hd.), tongue (Tg.), mouth (Mth.), shoulder (Shl.), elbow (Elb.), digits of hand (Dig.), abdomen (Abd.), hip, knee (Kn.), digits of foot (Dig.) in the posterior limb of the internal capsule ; O.C., fibres to the occipital lobes ; O.P., fibres to optic radiation ; S, sensory fibres.

medullares. [These striæ medullares are inexcitable to electrical stimuli.] Of the three masses of grey matter into which the ventricular nucleus is split up by the white fibres or striæ medullares, the inner and central ones (fig. 627, 3, 2) are

called the **globus pallidus** on account of their paler colour, while the outer one (fig. 627, 1) is called the **putamen.**]

The anterior limb of the internal capsule sweeps between the caudate and lenticular nucleus, while the posterior segment lies between the optic thalamus and the lenticular nucleus (fig. 626). External to the first division of the lenticular nucleus is the **external capsule** (figs. 626, 627), whose function is unknown. External to this is the **claustrum**, whose function is also unknown. It is evident that hæmorrhage into or about the basal ganglia is apt to involve the fibres of the internal capsule. [When the lenticulo-striate artery, or, as it is called, the "artery of hæmorrhage," ruptures (fig. 616, *a*SL), it may not only destroy the lenticular nucleus, but the internal capsule will be compressed; and the same is the case with the lenticulo-optic artery—the external capsule will tend to force the blood inwards. We know that in the **posterior limb** of the capsule the volitional or pyramidal fibres lie in the following order from before backwards—those for the face (and tongue) in the knee, in the anterior third those for the arm and hand, and in the middle third for the leg, and perhaps behind these those for the trunk (fig. 626), so that a very small lesion in this region will affect a large number of these fibres, converging as they do like the rays of a fan from the motor cortical areas where the arrangement of these centres is a supero-inferior one (fig. 614), to become an antero-posterior one in the knee and posterior limb of the internal capsule (fig. 626). The posterior third of this limb is sensory and is the "sensory crossway." This, however, is true only for the lowest levels of the capsule (*Beevor and Horsley*).]

[Horsley points out that hæmorrhage from the lenticulo-striate artery affects in order the muscles of the face, arm, leg, and trunk, while recovery is in the inverse order.]

[The **internal capsule** is composed of fibres converging through the corona radiata and coming from and going to the cortex cerebri; it varies in its shape in different parts of its course. It contains several sets of fibres, some of which are sharply marked off from their neighbours.]

[The arrangement of the fibres in the internal capsule in order from before back, and classified according to the region of the cortex with which they are connected, is—

1. Præfrontal.
2. Pyramidal or fronto-parietal.
3. Temporal.
4. Occipito-temporal.
5. Occipital.

The **præfrontal fibres** occur in the anterior limb of the internal capsule; they are inexcitable to electrical stimulation, and are certainly not efferent in function. They pass to the mesial side of the crus, and also to the sub-thalamic region. They degenerate when the frontal area is destroyed. The course of the pyramidal fibres has been stated already. The **temporal, occipito-temporal** and **occipital fibres** are inexcitable and seem to be connected with the general and special senses (*Beevor and Horsley*).]

[The fibres of the **pyramidal tract** arise in the motor areas (§ 378) of the cortex, and converge to form that part of the internal capsule which in a horizontal section, such as is shown in fig. 626, go to form the knee and the anterior two-thirds of the posterior limb of the capsule. The fibres from the several motor areas occupy definite positions in the capsule (fig. 626), and it is to be noted that while the arrangement of the cortical motor areas is hardly a vertical one, the corresponding tracts have an anterior posterior or fore and aft arrangement in the internal capsule, as seen in a horizontal section. Traced from the capsule, they run into the pes, and occupy its central and larger portion, being bounded internally by a median

strand of fibres and externally by another group of fibres. From the pes they pass into the pons, where they are split up into a number of bundles interlacing with the deeper transverse fibres of the pons. In the pons some of the fibres form connections with certain of the nerve nuclei, *i.e.*, with the nuclei of the motor cranial nerves, and the remainder of the fibres proceed onwards to the bulb to form its anterior pyramids. The prolongation of these to the cord is given in § 365. Thus it is evident that there is a set of cranial pyramidal fibres and a spinal set.]

[**Anterior** or **fronto-cortical fibres.**—The frontal convolutions lying anterior to the motor areas also send fibres to the corona radiata, which converge and enter the anterior limb of the internal capsule (fig. 626). Thence they enter the crus and occupy its small median part. They can be traced through the pons, lying internal to the pyramidal fibres, and they seem to end in the pons, ending perhaps in the grey matter of the pons. Perhaps they are connected by transverse fibres in the pons with the cerebellum. They degenerate in a downward direction. These fibres are called the **fronto-pontine** or **fronto-cerebellar fibres.**]

[**Posterior** or **Temporo-occipito-cortical fibres.**—Fibres pass from the temporal and occipital regions to the internal capsule, and occupy its posterior third or thereby behind the pyramidal fibres; they pass into the pons and occupy its outer part and appear to end in the grey matter of the pons. These three tracts undergo descending degeneration, and their trophic centres are the cells of the cortex cerebri.]

[Some fibres arise in the nucleus caudatus, and can be traced as a descending tract as far as the pons, but lying dorsal to the previously mentioned tracts.]

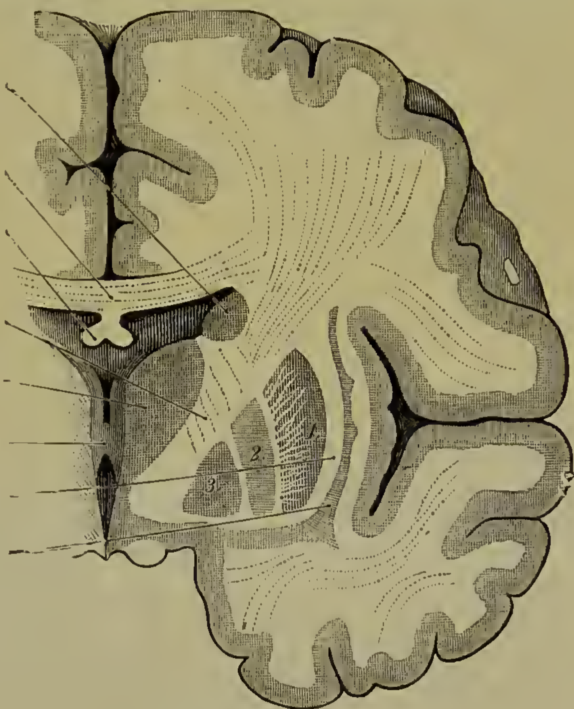


Fig. 627.

Frontal section through the right cerebral hemisphere in front of the soft commissure (posterior surface of the section).

[**Corona radiata.**—Although the internal capsule is chiefly made up of fibres that enter the crusta, still there are other fibres coming from the cortex, which form part of the corona radiata, but which, however, do not enter the crusta. Some fibres coming from the frontal and parietal areas of the brain converge to the extreme anterior end of the anterior limb of the internal capsule in front of the fronto-pontine fibres, and appear to end in the optic thalamus. Passing from or to the occipital and temporal regions, but chiefly the former, are fibres which lie at the tip of the posterior limb of the internal capsule, and are for the most part the fibres which form the **optic radiation** of Gratiolet. They enter the optic thalamus. But some fibres pass to the optic thalamus without entering the internal capsule. Thus the optic thalamus has wide and extensive connections with the cortex, so that other parts of the nervous system connection with the thalamus may thus indirectly be brought into connection with the cortex cerebri.]

[The **crura cerebri** (fig. 564, P), or cerebral peduncles, are two thick strands as they emerge above the pons, and as they are much larger than the pyramidal tracts, they must receive many fibres within the pons. A transverse section (fig. 628) shows that on them posteriorly, and connecting them, are the corpora quadrigemina (CQ). The crus proper is divided by the substantia nigra (SN) into a lower ventral part, the **crusta, pes,** or basis, and an upper dorsal part, or **tegmentum.** The crusta is composed exclusively of ascending and descending nerve-fibres, which can be traced from the cerebrum to the pons, bulb, and spinal cord. But the tegmentum, in addition to many nerve-fibres, contains much grey matter with nerve-cells. Near the middle of the tegmentum is the "**red nucleus**" or "tegmental nucleus" (RN). Outside this is the **fillet** (F), a well-defined bundle of nerve-fibres running upwards from the pons. Above the nucleus, near the middle line, is the "**posterior longitudinal bundle**" (p. l. b.), which is triangular in section. Above the tegmentum lie many nerve-cells, the origin of the third nerve (III), and arranged around the iter is much grey matter. The tegmentum itself ends partly in the optic thalamus, and partly in the sub-thalamic region, *i.e.*, ventral to the optic thalamus.]

[The **fillet** arises in the inter-olivary layer of the bulb from fibres derived from the supra-pyramidal or sensory decussation; the fibres come from the clava and caudate nuclei of the opposite side (p. 804). As it runs upwards, it joins the tegmentum, and receives accessions of fibres in its course from the grey matter of the pons. Some of its fibres—lateral—appear to end in the posterior corpus quadrigeminum, and others in the white matter below the anterior corpus quadrigeminum; the median fibres pass onwards, some to end in the sub-thalamic region, others in the optic thalamus, and others again appear to be continued on to the cortex.]

[The **posterior longitudinal bundle** appears to be a continuation upwards of some of the fibres of the anterior ground-bundle of the anterior column of the cord; it runs dorsal to the formatio reticularis of the bulb. It perhaps gives origin to part of the nuclei for the nerves of the eyeball.]

The **pes** or **crusta** of the cerebral peduncle when traced onwards gradually rises more dorsally, and spreads out like a hollow case, with the convexity looking outwards, forming between the optic thalamus and caudate nucleus internally and the lenticular nucleus externally the internal capsule. The **internal capsule** necessarily varies in its shape according as it is viewed in a vertical transverse (fig. 627) or sagittal or horizontal section of the brain (fig. 626), the fibres of the internal capsule diverge from each other, forming part of the **corona radiata**, which radiates to all parts of the cortex cerebri.]

Injury to **one cerebral peduncle** causes, in the first place, violent pain and spasm of the opposite side, while the blood-vessels on that side contract, and the salivary glands secrete. These phenomena of irritation are followed by paralytic symptoms of the *opposite* side, viz., anæsthesia (§ 365) and paresis, or incomplete voluntary control over the muscles, as well as paralysis of the vaso-motor nerves. In affections of the cerebral peduncle in man, we must remember the relation of the oculo-motorius to it, as the latter is often paralysed on the *same* side [while the extremities, tongue, and half the face are paralysed on the opposite side from the lesion].

The **middle third** of the **crusta** of the cerebral peduncle (fig. 502) includes the direct pyramidal tracts (§§ 365, 378). The fibres of the **inner third** connect the frontal lobes with the cerebellum through the superior cerebellar peduncles. In the **outer third** are fibres which connect the pons with the temporal and occipital cerebral lobes (*Flechsig*). The fibres which pass from the tegmentum into the corona radiata conduct sensory impulses (*Flechsig*).

[The **pons Varolii** contains ascending and descending fibres, as well as transverse ones, and, in addition, the continuation upwards of grey matter from the medulla, special masses of grey matter, and the nuclei of certain cranial nerves. Its appearance in section necessarily varies with the region where the section is made.

Fig. 629 is a transverse section through part of the seventh nerve. The lower part shows the superficial (s.t.f.) and deep (d.t.f.) transverse fibres, with the pyramidal fibres (Py) between them.]

Stimulation or section of the pons causes pain and spasms; after the section, there may be sensory, motor, and vaso-motor paralysis, together with forced movements. For diagnostic purposes in man, it is important to observe if alternate hemiplegia be present.

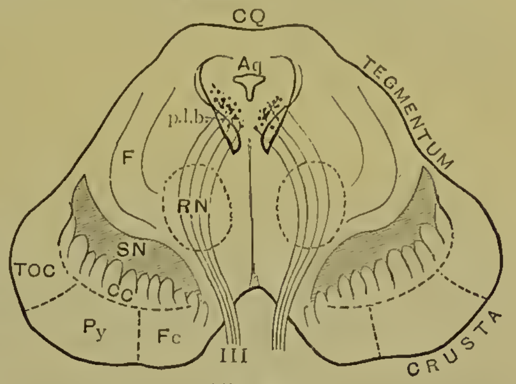


Fig. 628.

Scheme of transverse section of the cerebral peduncles. CQ, corpora quadrigemina; Aq, aqueduct; p.l.b., posterior longitudinal bundle; F, fillet or lemniscus; RN, red nucleus; SN, substantia nigra; III, third nerve; Py, pyramidal tracts; Fc, fronto-cerebellar; and TOC, temporo-occipital fibres of the crusta; CC, caudate-cerebellar fibres in upper part of crusta (after *Wernicke and Gowers*).

[In lesions situated in the **lower half** of one side of the pons, there is facial paralysis on the same side as the lesion and paralysis (motor and sensory, and more or less complete) on the opposite side of the body—this is called **alternate paralysis**; while, if the lesion be in the **upper half** of one side of the pons, the facial paralysis is on the same side as the paralysis of the body. But the parts supplied by the 5th and 6th nerves may also be involved. This is explained by fig. 630, where the upper facial fibres cross in the pons. Sudden and extensive lesions of the pons are frequently associated with hyperpyrexia, the temperature often rising rapidly within an hour, perhaps from the grey matter in the floor of the 4th ventricle being affected; but whether it is due to some effect on a heat-regulating or heat-producing centre is uncertain. **Tumours** of considerable size may press on the pons without producing very marked symptoms, as tumours tend to push aside tissues, unless they be infiltrating in their character. Lesions of the transverse superficial fibres (**middle cerebellar peduncles**) often give rise to involuntary forced movements, there being a tendency to move to one side or the other.]

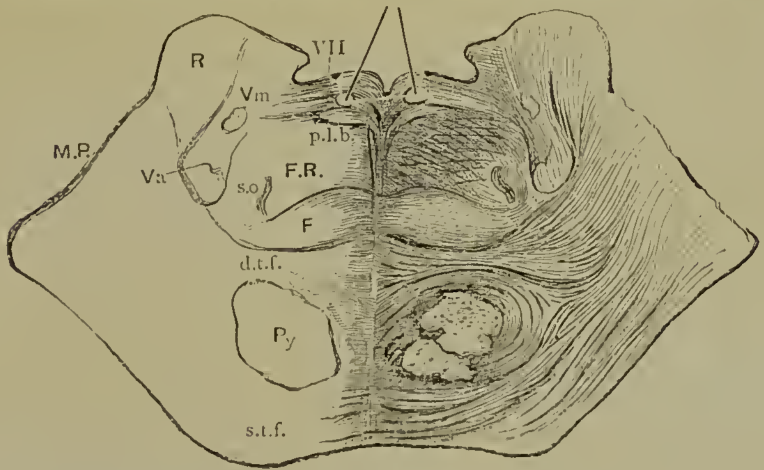


Fig. 629.

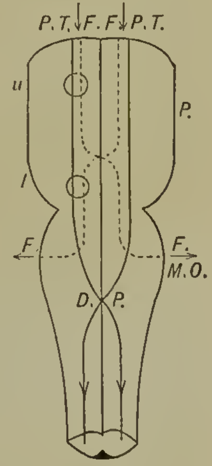


Fig. 630.

Fig. 629.—Tranverse section of the pons through part of the seventh nerve. ×2. F.R., formatio reticularis; VII, seventh nerve; Va, ascending root, and Vm. motor root of the fifth nerve; F, fillet; s.o., superior olive; s.l.b., superior longitudinal bundle; Py, pyramidal fibres; R, restiform body; M.P., middle peduncles of cerebellum; d.t.f. and s.t.f., deep and transverse superficial fibres of the pons (after *Wernicke*). Fig. 630.—Scheme of the fibres in the pons; PT, pyramidal tracts; F, facial fibres; *u*, upper, *l*, lower lesion; MO, medulla oblongata; DP, decussation of pyramids.

[**Corpora quadrigemina.**—The **anterior brachium** arises from the grey matter of each corpus, and passes downwards and forwards to join the external corpus geniculatum and help to form the optic tract, but some of its deeper fibres pass to-

wards the thalamus, and from it to the corona radiata, and so on to the cerebral cortex. The **posterior** brachium passes to the internal geniculate body, whence it is continued on to the tegmentum.]

Destruction of the corpora quadrigemina.—*On one side* in mammals (or their homologues, the optic lobes in birds, amphibians, and fishes) causes actual *blindness*, which may be on the same or the opposite side, according to the relation of the fibres crossing at the optic chiasma (§ 344). *Total* destruction causes blindness of both eyes. At the same time the reflex contraction of the pupil, due to stimulation of the retina with light, no longer takes place (*Flourens*), where the optic is the afferent and the oculomotorius the efferent nerve (§ 345). If the cerebral hemispheres alone be removed, the pupil still contracts to light, as well as after mechanical stimulation of the optic nerve (*H. Mayo*). Destruction of the corpora quadrigemina interferes with the complete harmony of the motor acts; disturbance of equilibrium and inco-ordination of movements occur (*Serres*). In frogs, Goltz observed not only awkward, clumsy movements, but at the same time the animals have to a large extent lost the power of completely balancing the body (p. 844). A similar result was observed in pigeons (*M'Kendrick*) and rabbits (*Ferrier*). Extirpation of the eyeball is followed by atrophy of the opposite anterior corpus quadrigeminum (*Gudden*).

According to Bechterew, the fibres of one optic tract pass through the anterior brachium (fig. 626) into the anterior pair (nates) of the corpora quadrigemina; while those fibres which cross in the chiasma (fig. 514) pass into the posterior pair (testes). According to this arrangement we have partial blindness, according as one or other pair of these bodies is destroyed.

[In man, very little is known regarding the effects of disease of the corpora quadrigemina, interference with the ocular muscles being the most marked symptom; but the inco-ordination of movement which has been observed may be due to pressure upon the superior cerebellar peduncle, while it is by no means certain that the defects of vision are directly due to lesions of these bodies.]

Stimulation of the Corpora Quadrigemina.—The corpora quadrigemina react to electrical, chemical, and mechanical stimuli. The results of stimulation are very variously stated. According to some observers, there is dilatation of the pupil on the same side; according to Ferrier, it may be the pupil on the opposite or on the same side. The stimulation may be conducted from the corpora quadrigemina to the medulla oblongata, and to the origin of the sympathetic, for, after section of the sympathetic nerve in the neck, dilatation of the pupil no longer takes place. According to Knoll, the contraction of the pupil observed by the older experimenters occurs only when the adjoining optic tract is stimulated. Stimulation of the right anterior corpus quadrigeminum causes deviation of *both* eyes to the left (and conversely); on continuing the stimulation, the head is turned to this side. On dividing the corpora quadrigemina by a vertical median incision, stimulation of one side causes the result to take place only on one side (*Adamük*). Ferrier observed signs of pain on stimulating these organs in mammals. Carville and Duret conclude from their experiments that these organs are centres for the extensor movements of the trunk. Ferrier found, on stimulating one optic lobe in a pigeon, dilatation of the opposite pupil, turning of the head towards the other side and backwards, movement of the opposite wing and leg; strong stimulation caused flapping movements of both wings. Danilewsky, Ferrier, and Lauder Brunton observed a rise of the blood-pressure and slowing of the heart-beat, together with deeper inspiration and expiration.

Bechterew ascribes all the phenomena, except those of vision itself, which accompany injury or stimulation of these bodies, to affections of deeper-seated parts. He asserts that the corpora quadrigemina contain neither the centre for the movements of the pupils nor that for the combined movements of the eyeballs; not even the centre for maintaining the equilibrium of the body. Stimulation of these bodies causes the animals to perform marked movements. Reflex phenomena, nystagmus, forced movements, and unsteadiness of the gait only occur, however, when the deeper parts are injured.

Pathological.—Lesions of the anterior pair in man, according to the extent of the lesion, cause disturbance of vision, failure of the pupil to contract to light, and even blindness; there may be paralysis of the oculomotorii on both sides. Disease of the posterior pair may be associated with disturbances of co-ordination (*Nothnagel*).

Forced Movements.—It is evident from what has been said regarding the importance of the corpora quadrigemina for the harmonious execution of movements, that *unilateral* injury of such parts as are connected with them by conducting

channels, must give rise to peculiar unilateral disturbance of the equilibrium, causing variations from the symmetrical movements of both sides of the body. These movements are called *forced movements*. To this class belong the "**mouvements de manège**," where the animal, instead of moving in a straight line, runs round in a circle; **index movements**, where the anterior part of the body is moved round the posterior part, which remains in its place, just like the movements of an index round its axis; and **rolling movements**, when the animal rolls on its long axis. All these forms of movement may pass into each other, and they are, in fact, merely different varieties of the same kind of movement. The parts of the nervous system whose injury produces these movements are the corpus striatum, optic thalamus, cerebral peduncle, pons, middle cerebellar peduncles, and certain parts of the medulla oblongata. Eulenburg observed index movements in the rabbit, after injury to the surface of the brain, and Bechterew observed the same in dogs. Forced movements, together with nystagmus and rotation of the eyeballs, are caused by injury to the olives (*Bechterew*). The statements of observers vary as to the direction and kind of movement produced by injuring individual parts. The following observations have been made:—Section of the **anterior part of the pons**, and of the crura cerebelli causes index, or, it may be, rolling movements towards the other side; section of the **posterior** part of the same regions causes rolling movements towards the *same* side, while the same result is caused by a deeper puncture into the tuberculum acusticum, or into the restiform body. Section of one cerebral peduncle causes mouvements de manège, while the body is curved with the convexity towards the same side. The nearer to the pons the section is made the smaller is the circle described; ultimately index movements occur. Injury to one optic thalamus produces results similar to puncture of the anterior part of the cerebral peduncle, because the latter is injured along with it at the same time. Injury to the anterior part of one optic thalamus causes the opposite kind of forced movement, viz., with the concavity of the body towards the injured side. Injury to the spinal portion of the medulla oblongata is followed by bending of the head and vertebral column, with the convexity towards the injured side, along with movements in a circle. When the anterior end of the calamus and the part above it are injured, the movements are towards the sound side.

Strabismus and **Nystagmus**.—Amongst the forced movements may be reckoned deviation of the eyeballs, strabismus or squinting, and involuntary oscillation of the eyeballs, constituting *nystagmus*. The latter condition occurs after superficial lesions of the restiform body, as well as of the floor of the 4th ventricle. A unilateral, deep, transverse injury, from the apex of the calamus upwards as far as the tuberculum acusticum, causes the eye of the same side to squint downwards and forwards, that of the other side backwards and upwards. Section of both sides causes this condition to disappear (*Schwahn*). Hence, Eckhard assumes that the medulla oblongata is the seat of an apparatus controlling the movements of the eyes (*Eckhard*), which can be excited by sudden anæmia, *e.g.*, ligature of the cephalic arteries in a rabbit.

In pathological degeneration of the olivary body of the medulla oblongata in man, Meschede observed intense rotatory movements towards the *same* side.

Theory.—In order to explain the occurrence of forced movements, it is suggested that there is unilateral incomplete paralysis (*Lafarque*), so that the animal in its efforts to move onwards leaves the paralytic side slightly behind the other, and hence there is a variation from the symmetry of the movements. Brown-Séquard regards the matter in exactly an opposite light, viz., as due to stimulation from injury, causing an excessive activity of one-half of the body. Henle ascribes the movements to *vertigo*, or a feeling of giddiness caused by the injury. In all operations on the central nervous system, where the equilibrium is deeply affected, there is a considerable increase in the number and depth of the respirations (*Landois*).

Specially interesting is the cerebral *unilateral* **decubitus acutus** or bed-sore, described by Charcot, which always occurs on the paralysed side of the body, *i.e.*, on the side opposite to the cerebral injury. It begins on the second or third day, rapidly causes enormous destruc-

tion and sloughing of the tissues on the back and lower extremities, and death soon takes place. The decubitus which occurs after spinal injuries usually begins in the middle line of the buttocks, and extends symmetrically on *both* sides. In cases of unilateral injury to the spinal cord, the decubitus occurs on the *corresponding* side of the sacral region (p. 715).

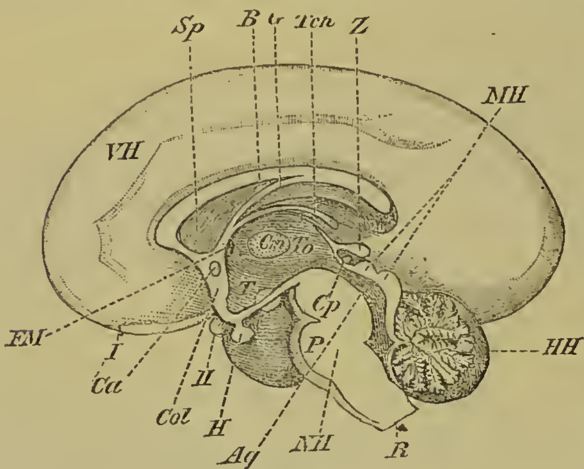


Fig. 631.

Longitudinal section of an adult human brain. *Aq*, aqueduct of Sylvius; *B*, corpus callosum; *Ca*, anterior commissure; *Cm*, middle commissure; *Col*, lamina terminalis; *Cp*, posterior commissure; *FM*, foramen of Munro; *G*, fornix; H, pituitary body; *HH*, cerebellum; *MH*, corpora quadrigemina; *NH*, medulla oblongata; *P*, pons Varolii; *R*, spinal cord; *Sp*, septum lucidum; *I*, infundibulum; *Tch*, tela choroidea; *To*, optic thalamus; *VH*, cerebrum; *Z*, pineal gland; *I*, olfactory lobe and nerve; *II*, optic nerve.

[The **Pineal Gland** or **epiphysis cerebri** lies on the back of, and is connected with, the third ventricle (fig. 631, *Z*). It projects backwards between the corpora quadrigemina. It is originally developed as a hollow outgrowth from that part of the embryonic brain which becomes the third ventricle. The hollow centre usually disappears, while the distal portion becomes enlarged and is often lobulated. Its distal portion may terminate outside the skull; and in some animals there is developed in the median line of the skull an eye—**pineal eye**—arranged on the invertebrate plan, as in Anguis, Hatteria, &c. (*De Graaf*, *Spencer*) (§ 405).]

[The **pituitary body** or **hypophysis cerebri** consists of two lobes, different in origin and structure (fig. 631, H). The *posterior lobe* is developed as a hollow outgrowth from the part of the embryonic brain connected with the third ventricle. It loses its cavity and its nervous tissue; is permeated by connective-tissue and blood-vessels; and is connected with the floor of the third ventricle by the infundibulum. The *anterior lobe* is developed as a tubular invagination of the stomodæum, *i.e.*, from the ectoderm of the buccal cavity; but it soon loses its connection with this cavity as the upper end enlarges, and the stalk atrophies. In mammalia, the upper expanded end unites with the anterior lobe to form the pituitary body. For the effects of its removal, see § 103, V.]

Increase of surface is obtained in the cerebellum by means of a number of leaf-like folds, each of which has a number of secondary leaflets or folds.

380. **STRUCTURE AND FUNCTIONS OF THE CEREBELLUM.**—[**Structure.**—On examining a vertical section of a cerebellar leaflet, we observe the following microscopic appearances;—Externally is the pia mater with its blood-vessels (fig. 632, *a*), which penetrate into the grey matter which forms a thin continuous layer on the surface; within is the medulla or central white matter, composed of white nerve-fibres. The **grey matter** consists of *b*, a broad outer or **molecular** layer (400 μ thick), largely composed of branched fibrils; and internal to it is *d*, the "**granular,**" or **nuclear**, or rust-coloured layer. On the boundary line between these two is the layer of Purkinje's cells, *c*. The **cells of Purkinje** form a single layer of large multipolar flask-shaped nerve-cells (40 μ by 30 μ), which have been compared to the branched antlers of a stag (fig. 633). From their outer surface is given off a process which rapidly divides, and gives rise to a large number of smaller processes running outwards in the outer grey layer. These processes branch to form fibrils, and the latter form part of the ground-plexus of fibrils in this layer. An unbranched axial cylinder process is sent inwards to the granular layer, which it traverses obliquely and becomes continuous with a nerve-fibre in the central white matter—every cell of Purkinje being continuous with a straight unbranched medullated nerve-fibre. The *unbranched* nerve-fibres run straight from the medulla through the granular layer, forming no connection with its granules. A second set of *branched* or anastomosing, often varicose, nerve-fibres, finer than the foregoing, pass from the medulla into the granular layer, where they form a network of fibrils which is continued into the molecular layer. This shows that the grey superficial matter of the cerebellum is connected with the central white matter by two sets of nerve-fibres. The **granular** or **nuclear layer** is composed of closely packed granules of two kinds; one is stained by hæmatoxylin, and the other with eosin (*Denissenko*). The hæmatoxylin stained cells are most numerous; they consist of a nucleus surrounded by protoplasm, and are what were formerly called granules. The eosin-stained cells, which are also stained by nigrosin (*Beevor*), are interposed in the course of medullated nerve-

fibres. The hæmatoxylin cells, called glia-cells by Beevor, have processes, and form a network throughout the granular layer, which also extends into the molecular layer. This network is regarded as the continuation of the modified myelin of the nerve-fibres, and it forms a capsule for the cells of Purkinje. The **molecular layer** consists of a ground substance, composed of a spongy network of fine fibrils, some of which seem to be of the nature of neuroglia, and others are nerve-fibrils. When these fibrils are cut across they give the layer its molecular dotted appearance. Some authors describe it as containing a homogeneous substance, part of which is more condensed to form a *limitans externa* on the surface of the cerebellum, while on the boundary line next the granular layer the branches of the glia-cells form a *limitans interna*, and between the two stretches the neuro-keratin network. Some small varicose nerve-fibres exist in this layer continuous with those in the granular layer. The branched process of the **cells of Purkinje** is fibrillated, and the finer processes are composed also of fibrils, which are gradually distributed until they become isolated. It is suggested by Beevor that these fibrils bend at a right angle in a plane parallel to the surface, and rearrange themselves as fibres surrounded by a medullated sheath, and that these fibres run inwards through the molecular and granular layers—as the branched fibres—to the medulla.]

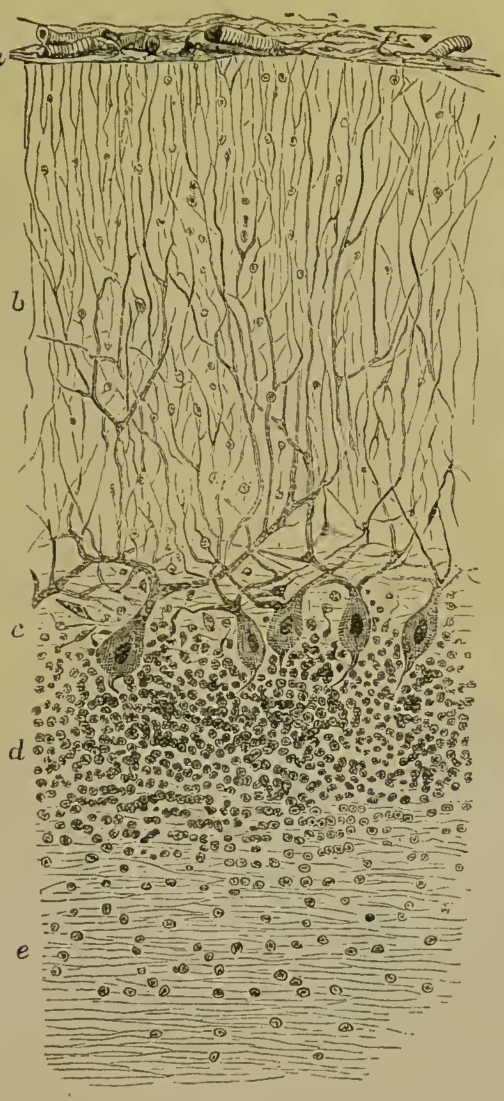


Fig. 632.

Fig. 633.

Fig. 632.—Vertical section of the cerebellum. *a*, pia mater ; *b*, external layer ; *c*, layer of Purkinje's cells ; *d*, inner layer ; *e*, medullary white matter. Fig. 633.—Purkinje's cell, sublimate preparation. × 120.

[**Results by Golgi's Method.**—It has been shown by Golgi, Ramón y Cayal and Kölliker that the nuclear layer contains a very large number of multipolar nerve-cells, some small and others large. From the smaller nerve-cells an axis-cylinder process proceeds vertically into the molecular layer where it divides into two horizontal and longitudinal unbranched fine fibres whose terminations are unknown. The larger cells occur more seldom, and their numerous branched protoplasmic processes penetrate deep into the molecular and central white matter.

In the molecular layer also are branched nerve-cells ; the innermost ones have been called "basket cells." They have numerous long protoplasmic processes, the

branches of some of which reach to the outer parts of the molecular layer. The axis-cylinder process is very long and runs transversely parallel to the cerebellar folds over the bodies of the cells of Purkinje, and sends inwards branches which rapidly split up and form a sort of basket-like plexus round the bodies of Purkinje's cells.]

Purkinje's cells give off an extraordinary number of protoplasmic processes, which pass quite to the surface of the molecular layer, but these processes never anastomose amongst themselves and they all lie in one plane, viz., in the transverse direction of the leaflet, so that the cell appears as in fig. 633 when the plane of ramification is directed to one, but if looked at on edge, they present the appearance seen in fig. 634. The processes end free. The axis-cylinder process gives off some lateral branches, some of which run backwards into the molecular layer. Numerous fine medullated branched nerve-fibres exist in the molecular layer, and they form a dense network in the granular layer under Purkinje's cells. Some of the nerve-fibres in the central white matter divide before they enter the grey matter.]

Fig. 634.
Purkinje's cell seen from the side, the section being made vertical to the surface and parallel with the long axis of a convolution.

Function of the Cerebellum.—Injuries of the cerebellum cause disturbances in the harmony of the movements of the body. Most probably the cerebellum is a great and important central organ for the finer co-ordination and integration of movements. The fact that it is connected with all the columns of the spinal cord and with all the central ganglionic masses renders this very probable. The direct cerebellar tracts from the lateral column of the cord conduct sensory impressions to the cerebellum, and thus indicate the posture of the trunk. The cerebellum may affect the motor nerves of the cord through fibres which pass downward in the lateral columns of the cord from the restiform bodies (*Flechsig*). Injury of the cerebellum neither produces disturbance of the psychical activities, nor does it interfere with the will or consciousness. Injuries to the cerebellum itself do not give rise to pain.

According to Schiff, the cerebellum does not actually regulate the co-ordination of movements. According to him, there is a mechanism on both sides of the middle line, which increases all the complicated muscular movements—not only those for powerful contractions, but also the peculiar fine movements which fix the limbs and joints. Luciani asserts that destruction of the cerebellum produces a condition of incomplete tonus, there being a want of energy to control the voluntary muscles. Each half of the organ acts on both halves of the body.

Injury or **Removal of Cerebellum.**—The immediate results produced by injury to or removal of the cerebellum have been admirably described by Flourens (fig. 635). On removing the most superficial layers in a **pigeon**, the animal merely showed signs of weakness and interference with the uniformity of its movements. On removing more of the cerebellum, the animal became greatly excited, and made violent irregular movements, which did not partake of the character of convulsions. The sensorium was unaffected, while vision and hearing were intact. Co-ordinated movements, such as walking, flying, springing, and turning, could be executed but imperfectly. After removal of the deepest layers, the power of executing the above-named movements was completely abolished. On placing the pigeon on its back, it could not get on its legs; at the same time it made continually the greatest exertions in its movements, but these were always inco-ordinated, and therefore without any satisfactory result. The will, intelligence, and perception remained intact; the animal could see and hear, and sought to avoid obstacles placed

in its way. It gradually exhausted itself in fruitless efforts to get on its legs, and ultimately remained in its abnormal position, quite exhausted. Flourens concluded from these experiments that the cerebellum is the centre for co-ordinating voluntary movements. Lussana and Morganti regard the cerebellum as the seat of the muscular sense.

[**Extirpation in Mammals.**—The dangers attending this operation are so great that but few animals survive. Luciani, however, by using antiseptic and other precautions, has been able to operate so that complete cicatrisation was obtained, the animal (young bitch) being restored to health for a few months. The cerebellum alone was removed, but not its peduncles. As in all other similar operations, we must distinguish sharply the phenomena manifested during recovery from those after complete recovery. During the *first period* of six weeks, from the time of the operation until complete recovery, the symptoms are those of injury and irritation of the divided peduncles, along with those resulting from the removal of the organ. They are clonic contractions of the muscles of the fore limb, neck, and back, passing into tonic contractions when the animal attempts to move, and also weakness of the hind legs, so that all the normal voluntary movements are interfered with, *i.e.*, inco-ordinated, although these symptoms may be explained by the injury to adjoining parts. There was no sensory disturbance or loss of the muscular sense, although closing the eyes rendered standing impossible. As recovery takes place, these symptoms disappear, and the animal enters on the *second period*, where the symptoms depending on the actual loss of the organ are pronounced. The contracture and pseudo-paralytic weakness disappear, while there are alterations in the tone of the individual muscles, producing a sort of "**cerebellar ataxy.**" The dog could swim in quite a normal manner, its power of equilibration was not interfered with, but acts requiring a greater development of muscular energy could not be properly executed. This period lasted four to five months. After this time its health gave way, there was otitis, conjunctivitis, articular and cutaneous inflammations, while a peculiar form of marasmus set in, and the animal died after eight months. In **fishes** also, the removal of the cerebellum does not affect their power of locomotion (*Baudelot*).]

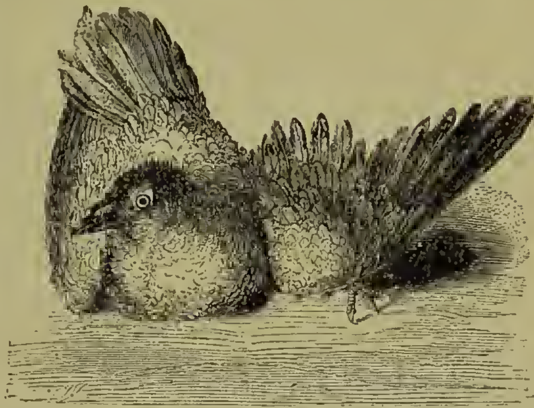


Fig. 635.
Pigeon with its cerebellum removed.

Duration of the Phenomena.—After superficial lesions, or after a deep incision, the disturbances of co-ordination soon pass away (*Flourens*). If the injury affects the lowest third of the cerebellum, the motor disturbances remain permanently. Symmetrical lesions do not disturb co-ordination (*Schiff*). After removing the greater portion of the cerebellum in birds, Weir-Mitchell has observed that the original disturbances gradually disappear; and *after months* only slight weakness and a condition of rapid fatigue remain.

After ablation of the cerebellum, **secondary degeneration** occurs in the part of the pons around the pyramids the lower olives, all the cerebellar peduncles, and the direct cerebellar tract, usually on the same side (*Flechsig*). It is found also in individual fibres in all the cranial nerves and the anterior roots of the spinal nerves (*Marchi*).

In the **dog**, superficial injuries of the vermiform process, or of one-half of the organ, produce merely temporary disturbances; while deep injuries to the vermiform process, or removal of one hemisphere and a part of the vermiform process, cause permanent rigidity of the legs and shaking of the head; if the worm and both halves are destroyed, there follows permanent pronounced disturbance of co-ordination (*v. Mering*). According to Baginsky, destruction of a large part of the vermiform process alone causes in mammals permanent disturbance of co-ordination. Ferrier found that a vertical section of the cerebellum in **monkeys** produced only inconsiderable disturbances of equilibrium; after injury of the anterior part of the middle lobe, the animal often falls forward; while, when the posterior part is injured, it falls backward. After injury of the lateral lobe, the animal is drawn towards the affected side (*Schiff*, *Vulpian*, *Ferrier*, *Hitzig*). If the middle commissure be injured, the animal rolls violently on its long axis towards the injured side (*Magendie*). Paralysis never occurs after injuries of the cerebellum, nor is there ever disturbance of sensation or of the sense of touch. Luciani found that, in animals with the cerebellum extirpated, marasmus ultimately set in. In **frogs**, an important

organ concerned with motion lies at the junction of the oblongata with the cerebellum (*Eckhard*). After it is removed the animal can no longer execute co-ordinated jumping movements, nor can it crawl (*Goltz*).

[In man the cerebellum is connected with the maintenance of the equilibrium. There may be a lesion of the hemispheres without any marked symptoms; but if the middle lobe be injured or pressed on by a tumour, there is usually a **reeling** or staggering gait, like that of a drunken man. Ross points out that if the tumour affect the upper part of this lobe, the tendency is to fall backwards, and if in the lower part, to fall forwards or to revolve round a horizontal axis. Vomiting is frequently persistent and well marked, while there may be nystagmus and tonic retraction of the head.]

After injuries of the cerebellum, involuntary oscillations of the eyeballs or **nystagmus**, as well as squinting (*Magendie, Hertwig*), have been observed; while Ferrier observed movements of the eyeballs after electrical stimulation. According to Curschmann, Eckhard, and Schwann, this occurs only when the medulla oblongata is involved (§ 379).

Effects of Electricity and Vertigo.—If an electrical current be passed through the head, by placing the electrodes in the mastoid fossæ behind both ears, with the + pole behind the right and the − pole behind the left ear, then on closing the current there is severe *vertigo*, and the head and body lean to the + pole, while the objects around seem to be displaced to the left. If the eyes be closed, while the current is passing, the movements appear to be transferred to the person himself, so that he has a feeling of rotation to the left (*Purkinje*). At the moment the head leans towards the anode, the eyes turn in that direction, and often exhibit nystagmus. The electrical current probably stimulates the nerves of the ampullæ, as we know that affections of these bodies cause vertigo (§ 350). The cerebellum has no relation to the sexual activities, as was maintained by Gall. The contractions of the uterus observed by Valentin, Budge, and Spiegelberg, after stimulation of the cerebellum, are as yet unexplained.

Pathological.—Lesions of one hemisphere may give rise to no symptoms; but if the middle lobe is involved, there is inco-ordination of movement, especially a tendency to fall, unsteady gait, and pronounced vertigo. Irritative lesions of the middle peduncle cause complete gyrating movements of the body around its axis, together with rotation of the eyes and head (*Nothnagel*).

381. **PROTECTIVE APPARATUS OF THE BRAIN.**—**The membranes.**—The **dura mater cerebralis** is intimately united to the periosteum of the cavity of the skull, while the spinal dura mater forms around the spinal cord a freely suspended long sac, fixed only on its anterior surface. It is a fibrous membrane, consisting of firm bundles of connective-tissue intermixed with numerous elastic fibres, and provided with flattened connective-tissue corpuscles and Waldeyer's plasma cells. The smooth, inner surface is covered with a layer of endothelium. It is but slightly supplied with blood-vessels, although they are more numerous in the outer layers; the lymphatics are numerous, while nerves whose terminations are unknown give to the dura its exquisite sensibility to painful operations on it. Pacinian corpuscles have been found in the dura over the temporal bone. The lymphatic **subdural space** (*Key and Retzius*) lies between the dura and the arachnoid, and between the pia and arachnoid is the **subarachnoid space** (fig. 636). These two spaces do not communicate directly. The delicate arachnoid, thin and partially perforated, poor in blood-vessels and without nerves, is covered on both surfaces with squamous endothelium. Only on the spinal cord is it separated from the pia, so that between the two lies the lymphatic subarachnoid space; over the brain, the two membranes are for the most part united together, except the parts bridging over the sulci between adjacent convolutions. The arachnoid passes from convolution to convolution without dipping into the sulci, while the pia dips into each sulcus (fig. 636, *a*). The **ventricles** of the brain communicate freely with the lymphatic subarachnoid space, but not with the subdural space. The pia consists of delicate bundles of connective tissue without any admixture of elastic fibres; it is richly supplied with blood-vessels and lymphatics, and carries nerves which accompany the blood-vessels into the substance of the brain. The lymphatics open into the subarachnoid space (§ 196).

Subarachnoid Fluid, or **cerebro-spinal fluid**, lies in the sub-arachnoid space, which is traversed by trabeculæ of connective tissue. Within the brain are a series of cavities called **ventricles**, which communicate one with another in a definite way. The fourth ventricle is lined by a layer of columnar epithelium, and covered in dorsally by a membrane and continuation of the pia mater, from the middle of which there hangs into the roof of the fourth ventricle two vascular processes composed of capillaries—the choroid plexuses of the fourth ventricle, which are comparable to the larger plexuses of the lateral ventricles. In this membrane is the **foramen of Magendie** and two other smaller foramina, whereby the fluid in the subarachnoid space communicates with that in the fourth ventricle; but the lymphatics of the nerve-sheaths can be injected from the subarachnoid space, so that there is direct continuity of the fluid in the ventricles of the brain with that in the subarachnoid space, perivascular spaces of the cerebral substance, and the perineural lymphatics of nerves. The average **quantity** is about 2 ounces, and if it be suddenly withdrawn, epilepsy or convulsions may be produced; or, if it be

rapidly increased in amount, coma may be produced. The base of the middle and posterior parts of the brain and the medulla oblongata do not rest directly on bone, but are separated by a distinct interval from their osseous case, an interval occupied by the cerebro-spinal fluid and traversed by trabeculæ, so that, as Hilton expresses it, this fluid forms a perfect water-bed for those parts, being sustained by the venous circulation and the elasticity of the dura. It has important mechanical functions, protecting delicate parts of the brain from injury; by distributing vibratory impulses it insulates the nerve-roots, and has important relations to the quantity of blood in the brain and the cerebral circulation (Chemical Composition, § 198).]

[**Spina bifida.**—Sometimes the laminæ of the vertebræ in the lumbar or other region of the spinal column are imperfectly developed, in which case the membranes project through as a tumour distended by cerebro-spinal fluid and covered by skin. The effects of rapid tapping or compressing the sac are readily studied in such cases.]

The **Pacchionian bodies**, or granulations, are connective-tissue villi, which serve for the outflow of lymph from the subdural and subarachnoid spaces into the sinuses of the dura mater, especially the longitudinal sinus. The subarachnoid space also communicates with the spaces in the spongy bone of the skull, and with the veins of the skull and surface of the face (*Kollmann*). The subdural space also communicates with the lymphatic spaces in the dura, while the latter communicate directly with the veins of the dura. Both the subdural and subarachnoid lymphatic spaces communicate with the lymphatics of the nasal mucous membrane. The space outside the dura of the spinal cord is called the **epidural space**, and may be regarded as lymphatic in its nature; the pleural and peritoneal cavities may be filled from it; but it does not communicate with the cavity of the skull. The plexuses of blood-vessels are surrounded by undeveloped connective-tissue. The telæ choroideæ in the new-born are still covered with ciliated epithelium.

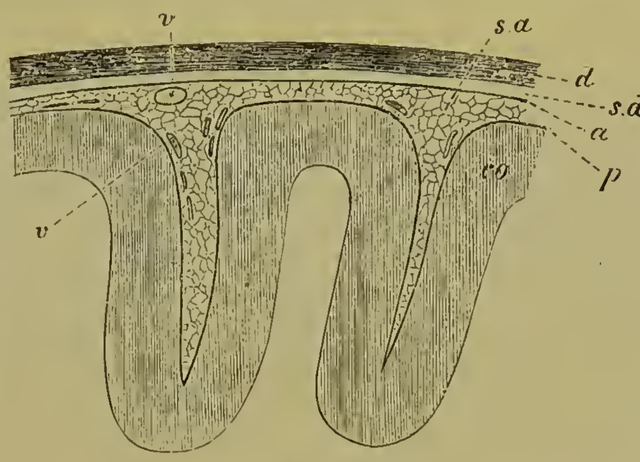


Fig. 636.

Vertical section of the cortex cerebri and its membranes; ×2½. *co*, cortex cerebri; *p*, intima piæ dipping into the sulci; *a*, arachnoid, connected with *p* by means of the loose subarachnoid trabeculæ in the subarachnoid space, *sa*; *v*, *v*, blood-vessels; *d*, dura; *sd*, subdural space.

Movements of the Brain.—The pulsations of the large basal cerebral vessels communicate their **pulsatile** movements (§ 79, 6) to the brain—the **respiratory** movements also affect it, so that the brain rises during expiration and sinks during inspiration. Lastly, there are slight alternating *vascular* elevations and depressions, occurring 2 to 6 times per minute, due to the periodic dilatation and contraction of the blood-vessels (§ 371). Psychical excitement influences these, and they are most regular during sleep. The movements are best seen especially where the membranes of the brain offer little resistance, *e.g.*, over the fontanelles in children, and where the membranes have been exposed by trephining. The presence of the cerebro-spinal fluid is most important for the occurrence of these movements, as it propagates the pressure uniformly, so that every systolic and expiratory dilatation of the blood-vessels is concentrated upon those parts of the cerebral membrane which do not offer any resistance (*Donders*). When the fluid escapes, the movements may almost disappear.

[**Methods.**—The following methods have been used by different observers in studying the **cerebral circulation**:—(1) Inspection of the pia mater (*Haller*), and the modification of this method by Donders, who trephined the skull, and inserted a glass plate in the aperture. (2) Over the fontanelles of children, or in cases of imperfect ossification of the skull bones, other observers have applied a receiving Marey's tambour, and thus recorded the movements of the brain synchronous with respiration and heart-beat (*Mosso*). (3) In the adult a hole is trephined in the skull, and a modified cannula inserted, and the movements of the brain recorded by means of a Marey's tambour (*Fredericq*). (4) Measuring the outflow of blood from a cerebral vein. (5) Measuring simultaneously the blood-pressure in the cerebral end of the divided internal

carotid artery, and in a systemic artery (*Franck*). (6) A plethysmographic method was used by Roy and Sherrington. A trepan hole is made in the skull, and the dura mater divided, and into the hole in the skull is fixed a metallic capsule, closed below by a flexible membrane, which rests on the surface of the brain, and follows its movements. The upper end of the capsule is connected with a recording apparatus, similar to that used for recording the volume of the kidney, or for studying the pulse-wave, in fact a kind of oncograph (p. 533). This method registers the variations in the vertical thickness of the cerebral hemisphere. At the same time it is most important to estimate the blood-pressure in a large vein and a systemic artery.]

[Stimulation of the central end of the sciatic nerve, and other sensory nerves, causes expansion of the brain, which is due to the rise of pressure in the systemic arteries, so that the expansion is due to the passive distention of the cerebral vessels as a result of the rise in the systemic blood-pressure.]

[Asphyxia also causes a great expansion of the brain, which is partly due to the passive distention of the cerebral vessels following on the rise of pressure in the systemic vessels, but partly also to active expansion of the cerebral vessels. Muscular movements also increase the cerebral congestion. The brain-curves exhibit Traube-Hering undulations under certain conditions. Chloral hydrate causes contraction of the brain, unaccompanied by any corresponding fall in the arterial blood-pressure. Chloroform causes marked cerebral contraction. Ether causes expansion, and strychnin an enormous expansion. Intra-venous injection of dilute acids produces great and immediate expansion of the brain, but there is no rise of pressure in the systemic arteries to account for the cerebral congestion ; alkalis diminish the volume of the brain. As a result of these and other experiments, it seems that the blood-supply to the brain varies directly with the blood-pressure in the systemic arteries. Roy and Sherrington, however, have found no evidence of the existence of vaso-motor nerves for the brain in the neck, or outside the cerebro-spinal canal or indeed in the medulla or cord. If there are vaso-motor fibres directly regulating the calibre of the vessels of the pia mater, there must be some other explanation of the adaptation of the state of the cerebral blood-vessel to the needs of the brain. Roy and Sherrington are inclined to think that the chemical products of cerebral metabolism can cause variations of the cerebral vessels, and thus the brain possesses an intrinsic mechanism by which its vascular supply can be varied locally in correspondence with local variations of functional activity, and this independent of the existence of vaso-motor nerve-fibres acting directly on the cerebral vessels, as is the case in other regions of the body.]

Mental excitement increases the pulsations of the brain. At the moment of awaking, the amount of blood in the brain diminishes ; sensory stimuli applied during sleep, so that the sleeper does not awake, increase the amount of blood. As the arteries within the rigid skull-case change their volume with each pulse-beat, the veins (sinuses) exhibit at every beat a pulsatile variation in volume, the opposite of that occurring in the arteries (*Mosso*).

The Cerebral Blood-Vessels.—The blood-vessels of the pia are said to be regulated by the vaso-motor nerves (§ 356, A, 3), and their calibre may also be influenced by the stimulation of more distant parts of the body (§ 347). Donders trephined the skull so as to make a round hole, and filled it with a piece of glass, so that with a microscope he could observe changes in the calibre of the blood-vessels. Paralysis of the vaso-motor nerves and narcotics dilate the blood-vessels ; they become greatly contracted at death (§ 373, I.). The blood-vessels are dilated during cerebral activity (§ 100, A), as well as during sleep. Increased pressure within the skull causes great derangement of the cerebral activity—laboured respiration (§ 368, B), unconsciousness even to coma, and paralytic phenomena—all of which may in part be referable to disturbances of the circulation. If all the cranial arteries be ligatured suddenly, there is immediate loss of consciousness, together with strong stimulation of the medulla oblongata and its centres, and death takes place rapidly with convulsions (compare § 373).

By the **free anastomosis** which takes place at the base of the brain, forming the **circle of Willis** (fig. 637), the individual parts of the brain are preserved from want of blood, when one or other blood-vessels is compressed or occluded. *Within* the brain the arteries are distributed as "**terminal** arteries," *i.e.*, the terminal branches of any one artery end in their own area, and do not anastomose with those of adjoining areas (*Cohnheim*). On the other hand, the peripheral arteries (arteries of the corpus callosum, Sylvian fissure, and deep cerebral) which run externally on the brain, form free anastomoses (*Tichomirow*).

[The **nutrient** or **ganglionic arteries** for the central ganglia arise in groups from the circle

of Willis, or from the first two centimetres of its trunks. The **antero-median** group (1) supplies the anterior part of the head of the caudate nucleus. The **postero-median** group (2) enter the posterior perforated space and supply the internal surface of the optic thalami and the walls of the third ventricle. The **antero-lateral** groups (3, 3) from the middle cerebral enter the anterior perforated space, supply the corpora striata, the anterior part of the optic thalamus, and the internal capsule. These branches are apt to rupture. The **postero-lateral** (4, 4) supply a large part of the optic thalami (*Charcot*). A line drawn at a distance of two centimetres outside the circle of Willis encloses the **ganglionic area**. The cerebral convolutions are supplied by the large branches of the circle of Willis. The **anterior cerebral** curves round the corpus callosum, and supplies the gyrus rectus and the supraorbital, the first and second frontal convolutions, the upper part of the ascending frontal, and the inner surface of the hemisphere as far as the quadrate lobule (fig. 637, I). The **posterior cerebral** goes to the region of the occipital lobe and the inferior aspect of the temporal lobe; the **middle cerebral** or **Sylvian** artery divides into four branches, which go to the posterior part of the frontal lobe, ascending frontal, and to all the parietal lobes, *i.e.*, chiefly to the motor areas (III) the angular gyrus, and to the first temporo-sphenoidal lobule. The terminal branches of these ganglionic arteries do not anastomose with the cortical system [although this seems to be subject to variations]. Fig. 638 shows the ganglionic arteries piercing the basal ganglia. Obviously, when hæmorrhage of the lenticulo-striate artery or "**artery of hæmorrhage**" (4, 4) occurs, it will compress the lenticular nucleus, or tear it up, and may even injure the parts outside, such as the external capsule, claustrum (T), and island of Reil (R), or those inside, *e.g.*, the internal capsule.]

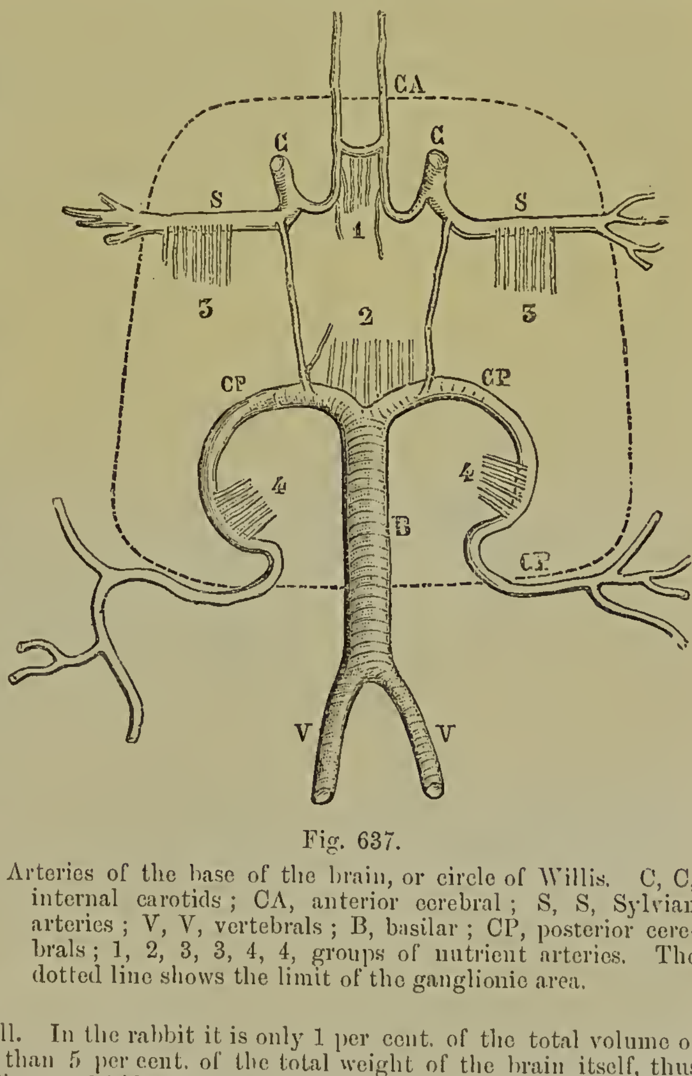


Fig. 637.

Arteries of the base of the brain, or circle of Willis. C, C, internal carotids; CA, anterior cerebral; S, S, Sylvian arteries; V, V, vertebrals; B, basilar; CP, posterior cerebrals; 1, 2, 3, 3, 4, 4, groups of nutrient arteries. The dotted line shows the limit of the ganglionic area.

[Thus the **anterior cerebral** supplies the prefrontal area and a small part of the motor area, that for the leg-centre in the paracentral lobule and upper end of the ascending frontal (and perhaps that for the trunk). The **posterior cerebral** supplies the centre for vision, and that connected with the course of the posterior part of the optic expansion, and also the sensory part of the internal capsule. The **middle cerebral** supplies the motor areas of the cortex, except part of the leg-centre and the basal ganglia, the auditory centre, and that for speech.]

[The **cerebral circulation** has many peculiarities. For its size, the percentage of blood in the brain at any one time is small. In the rabbit it is only 1 per cent. of the total volume of blood of the body, and not more than 5 per cent. of the total weight of the brain itself, thus forming a sharp contrast to the liver and kidney as regards blood-supply. The curves on the arteries serve to modify the effect of the cardiac shock, the circle of Willis permits within limits a free circulation; but, in as far as the skull is largely a rigid box, it was at one time taught that, as the brain substance and its fluids were practically incompressible, it was impossible to alter the amount of blood in the brain. This is a mistake. The amount of blood undergoes an alteration in this way, that when more blood passes in, some cerebro-spinal fluid moves out, and *vice versâ*, so that there is an intimate relation between these fluids. The sinuses form reservoirs for blood, and have much to do with the adjustment of the relative quantities of blood in the cerebral arteries and veins. They are easily filled, and more easily emptied, to

permit of more arterial blood being supplied to the brain. In the developing skull, the cerebro-spinal fluid may accumulate in large amount within the ventricles, and greatly distend both them and the yielding skull-case from internal pressure, as in **acute hydrocephalus.** The peculiarities and independence of the cortical and ganglionic arteries have already been referred to. Plugging by means of a clot, vegetation, or wart, carried from the heart, is common in the left middle cerebral artery.—Why?—When the plug is washed away by the blood-stream, owing to the left carotid springing from the aorta nearly in line with the blood-current, the plug readily passes into the left carotid and so into the left middle cerebral which is in line with the internal carotid. In such a case the convolutions and parts supplied by it are suddenly deprived of blood with immediate and serious results.]

[The **venous circulation** is peculiar. The sinuses are really spaces between the layers of the tough dura mater, and partly bounded by bone. The blood moves in the longitudinal sinus from before backwards, but most of the cortical veins open into it in a forward direction, so that their stream is opposed to that in the sinus. Thus, the blood which enters the brain by ascending arteries reaches the sinuses by ascending veins, the reverse of what obtains elsewhere, in parts where ascending veins convey blood from descending arteries, whereby the hydrostatic pressure and gravity aid the circulation, but here gravitation is opposed to the flow of blood in the cerebral veins. This will help to explain the occurrence of thrombosis in these vessels. Some of the veins on the surface communicate with intracranial veins, *e.g.*, those of the nose, the facial through the ophthalmic, mastoid veins and veins of the diploe. Hence, morbid processes affecting the scalp (erysipelas), ear (caries), or face (carbuncle) may readily affect intracranial structures (*Gowers*).]

If a person who has been in bed for a long time, and whose blood is small in amount, be suddenly raised into the erect position, cerebral anæmia is not unfrequently produced, owing to hydrostatic causes. At the same time, there may be loss of consciousness and impairment of

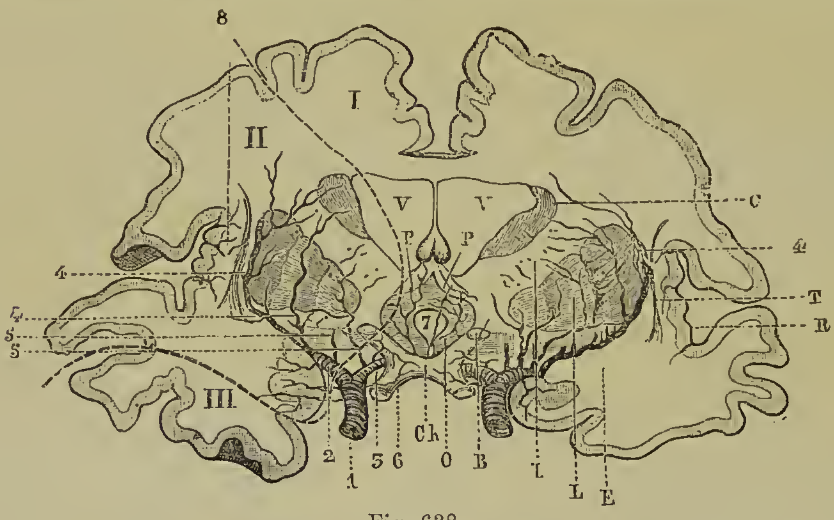


Fig. 638.

Transverse section of the cerebrum behind the optic chiasma. Arteries of the corpus striatum. C *h*, optic chiasma; B, section of optic tract; L, lenticular nucleus; I, internal capsule; C, caudate nucleus; E, external capsule; T, claustrum; R, convolutions of the island of Reil; V, V, section of the lateral ventricles; P, P, pillars of the fornix; O, grey substance of the third ventricle. Vascular areas—I, anterior cerebral artery; II, Sylvian artery; III, posterior cerebral artery; 1, internal carotid; 2, Sylvian, 3, anterior cerebral artery; 4, 4, lenticulo-striate arteries; 5, 5, lenticular arteries.

the senses. Liebermeister regards the *thyroid gland* as a collateral blood-reservoir which empties its blood towards the head during such changes of the position of the body. Perhaps this may explain the swelling of the thyroid as a compensatory act, when the heart beats violently, and the brain is surcharged with blood (§§ 103, III., and 371). Very violent muscular exertion, as well as marked activity of other organs, causes a very considerable fall of the blood-pressure in the carotid.

Pressure on the Brain.—The brain and the fluid surrounding it are constantly subjected to a certain mean *pressure*, which must ultimately depend upon the blood-pressure within the vascular system. The investigations of Naunyn and Schreiber on the *cerebral pressure* (or cerebro-spinal pressure) showed that the pressure must be slightly less than the pressure within the carotid, before the symptoms proper to pressure on the brain occur. These are, sudden attacks of headache, with vertigo, or it may be loss of consciousness, vomiting, slowing

of the pulse, slow and shallow respiration, convulsions—while the pressure of the cerebro-spinal fluid is increased. The cause of these phenomena lies in the anæmia of the brain. If the pressure is moderate, the above-named symptoms may remain latent; nevertheless, disturbances of the nutrition of the brain occur, with consecutive phenomena, such as persistent slight headache, feeling of vertigo, muscular weakness, and disturbances of vision (owing to neuro-retinitis with choked disc). Increase of the blood-pressure diminishes the symptoms, while diminution of the blood-pressure causes more pronounced phenomena of cerebro-spinal pressure. In the dog, *pain* begins with a pressure of 70 to 80 mm. Hg. *Consciousness is abolished* when the pressure is higher, and at 80 to 100 mm. *spasms* take place. A pressure of 100 to 120 mm. causes *slowing of the pulse*, owing to stimulation of the vagus at its origin; the respirations are temporarily accelerated and then diminish. Long-continued severe compression always, sooner or later, ends fatally. The blood-pressure at first is increased, owing to reflex stimulation of the vaso-motor centre from the pressure stimulating the sensory nerves; ultimately, the blood-pressure falls, and the pulse becomes very slow. Irregular variations in the blood-pressure point to a direct central stimulation of the vaso-motor centre by pressure. The application of continued slowly increasing pressure compresses the brain (*Adamkiewicz*). At the level of the cauda equina the pressure of the sub-arachnoid fluid = 7·5–12 mm. Hg in the dog (*Naunyn*).

382. **COMPARATIVE—HISTORICAL.**—**Comparative.**—Nerves are absent in the **protozoa.** Neuro-muscular cells occur in the **cœlenterata**, in the hydroida and medusæ, and they are the first indications of a nervous apparatus (§ 296). The umbrella of the medusa is covered with a plexus of nerve-fibrils, which at various parts along its margin is provided with small cellular thickenings corresponding to ganglia, and from these nerve-fibres proceed to the sense organs. Many of the **worms** possess a nervous ring in the cephalic portion, and in those provided with an intestine a single or double nervous cord, in the form of a ring, surrounds the pharynx. Branches (often two) pass from this into the elongated body, and usually these carry ganglia corresponding to each ring of the body of the animal. In the leech, only one gangliated cord is present. In the **echinodermata**, a large nerve-ring surrounds the mouth; and from it large nerves proceed, corresponding to the chief trunks of the water-vascular system. At the points where the nerves are given off, the nervous ring is provided with the so-called "ambulacral brains." The **arthropoda** are provided with a large cephalic ganglion placed above the pharynx, from which nerves pass to the sense organs. Another ganglion lies on the under surface of the pharynx, and is connected with the former by commissures. The pharynx is thus embraced by a gangliated ring, and from it proceeds the abdominal gangliated double chain, along the ventral surface of the body, through the thorax and abdomen. Sometimes several ganglia unite to form a large compound ganglion, while, in other cases, each segment of the body contains its own ganglia. In the **mollusca**, the œsophageal nervous ring is present, although the ganglionic masses vary much in position within it. A number of compound ganglia lie scattered in different parts of the body, and are united by nerves to the former. They represent the sympathetic system. In the **cephalopoda**, the œsophageal ring has almost no commissure, and a part of the ganglionic matter is enclosed in a cartilaginous capsule, and is often spoken of as a "brain." Additional ganglia are found in the mantle, heart, and stomach. In **vertebrates**, the nervous system invariably lies on the dorsal aspect of the body. In the amphioxus, there is no separation into brain and spinal cord. (See §§ 374 and 375.)

Historical.—Alkmaon (580 B.C.) placed the seat of consciousness in the brain; Galen (131–203 A.D.) regarded it as the seat of the impulses for voluntary movements. Aristotle (384 B.C.) ascribed the relatively largest brain to man; he stated that it was inexcitable to stimuli (insensible). One of the functions he ascribed to the brain was to cool the heat ascending from the heart. Herophilus (300 B.C.) gave the name calamus scriptorius; and he regarded the 4th ventricle as the most important organ for the maintenance of life. Even in Homer there are repeated references to the dangers of injuries of the neck. Aretaeus and Cassius Felix (97 A.D.) were aware of the fact that lesion of one cerebral hemisphere caused paralysis on the opposite side of the body. Galen was acquainted with the path in the spinal cord connected with movement and sensation. Vesalius (1540) described the five ventricles of the brain. R. Colombo (1559) observed the movements of the brain isochronous with the action of the heart. A more careful description of these movements was given by Riolan (1618). Coiter (1573) discovered that an animal can live after removal of its cerebrum. About the middle of the 17th century, Wepfer discovered the hæmorrhagic nature of apoplexy. Schneider (1660) estimated the weight of the brain in different animals. Mistichelli (1709) and Petit (1710) described the decussation of the fibres of the spinal cord below the pons. Gall discovered the partial origin of the optic nerve from the anterior pair of the corpora quadrigemina, and by dissecting the brain from below, he attempted to trace the course of the nerve-fibres to the convolutions (1810). Rolando described more accurately the form of the grey matter of the spinal cord. Carus (1814) discovered the central canal. The most compendious work on the brain was written by Burdach (1819–1826). The more recent observations are referred to in the text.

Physiology of the Sense Organs.

383. **INTRODUCTORY OBSERVATIONS.** — **Requisite Conditions.** — The **sense organs** have the function of transferring to the sensorium impressions of the various phenomena of the external world; they are, in fact, the intermediate instruments of *sensory perceptions.* In order that this may occur, the following conditions must be fulfilled:—(1) The sense organ, provided with its specific **end-organ,** must be anatomically perfect, and capable of acting physiologically. (2) A "**specific stimulus**" must be present, which under normal conditions acts upon the end-organ. (3) The sense organ must be connected with the cerebrum by means of a nerve, and the conduction through this path must be uninterrupted. (4) During the act of stimulation, the psychical activity (attention) must be directed to the process, and then the **sensation** results, *e.g.*, of light or sound, through the sense organ. (5) Lastly, when, by a psychical act, the sensation is referred to the external cause, then there is a conscious sensory perception. Often however, this relation is completed as an unconscious conclusion, as it is essentially a deduction from previous experience.

Stimuli.—With regard to the stimuli which are applied to the sensory apparatus, we distinguish:—(1) **Adequate** or **homologous** stimuli, *i.e.*, stimuli for whose action the sense organs are specially adapted, such as the rods and cones of the retina for the vibrations of the ether. Thus, each sense organ has a specific form of stimulus best adapted to act upon it. This is what Johannes Müller called the "**law of specific energy.**" (2) There are many other forms of stimuli (mechanical, thermal, chemical, electrical, internal somatic) which act upon the sense organs, producing the flash of light beheld when the eye is struck; singing in the ears when there is congestion of the head. These **heterologous** stimuli act upon the nervous elements of the sensory apparatus along their *entire* course, from the end-organ to the cortex cerebri. The homologous stimuli, on the other hand, act only on the end-organ, *i.e.*, light has no effect whatever upon the trunk of the exposed optic nerve.

Liminal Intensity.—Homologous stimuli act upon the sensory organs only within certain limits as to **strength.** Very feeble stimuli at first produce no effect. That strength of stimulus which is just sufficient to cause the first trace of a sensation is called by Fechner the "**liminal intensity**" of the sensation. As the strength of the stimulus increases, so also do the sensations, but the sensations increase equally when the strength of the stimulus increases in relative proportions. Thus, we have the same sensation of equal increase of light when, instead of 10 candles, 11, or instead of 100 candles, 110 are lighted—the proportion of increase in both cases is equal to one-tenth. As the logarithm of the numbers increases in an equal degree, when the numbers increase in the same relative proportion, the law may be expressed thus:—"The sensations do not increase with the absolute strength of the stimuli, but nearly as the logarithm of the strength of the stimulus." This is *Fechner's* "**psycho-physical law,**" but its accuracy has recently been challenged by E. Hering. [It holds good only with regard to stimuli of medium strength.] If the specific stimulus be too intense, it gives rise to peculiar painful sensations, *e.g.*, a feeling of blindness or deafness, as the case may be. The sense

organs respond to adequate stimuli, but only within certain *limits* of the stimulus, *e.g.*, the ear responds only to vibrating bodies emitting a certain range of vibrations per second; the retina responds only to the vibrations of the ether between red and violet, but not to the so-called heat vibrations or to the chemically active vibrations.

[It was Weber who worked out the relation between the intensity of stimuli and the changes in the quantity of the resulting sensations. He used the method of "least observable differences," as applied to sensations of pressure and the measurements of lines by the eye. Hence, it is called **Weber's Law**; but Fechner expanded it and assumed that all just observable differences are equally great, and so the law is sometimes called by his name.]

[**Fechner's Law.**—Expressed in another way, the result depends on (1) the strength of the stimulus, and (2) the degree of excitability. Supposing the latter to be constant, while the former is varied, it is found that if the stimulus be doubled, tripled, or quadrupled, the sensation increases only as the *logarithm of the stimulus.*]

[Suppose the stimulus to be increased 10, 100, or 1000 times, then the sensation increases only as 1, 2, or 3. Just as there is a *lower limit of excitation liminal intensity* (or *threshold*), so there is an upper limit or *maximum of excitation* or *height* of sensibility, when any further increase produces no appreciable increase in the sensation. Thus, we do not notice any difference between the central and peripheral portion of the sun's disc, though the difference of light intensity is enormous (*Sully*). Between these two is the *range of sensibiliy* (*Wundt*). There is always a constant ratio between the strength of the stimulus and the intensity of the sensation. The stronger the stimulus already applied, the stronger must be the increase of the stimulus in order to cause a perceptible increase of the sensation (**Weber's Law**). The necessary increment is proportional to the intensity of the stimulus, and it varies for each sense organ. If a weight of 10 grams be placed in the hand, it is found that 3·3 grams must be added or removed before a difference in the sensation is perceptible; if 100 grams are held, 33·3 grams must be added or removed to obtain a perceptible difference in the sensation. The magnitude of the fraction indicating the increment of stimulus necessary to obtain a perceptible difference of the sensation, is spoken of as the *constant proportion* or the *discriminative* sensibility. In the above case it is 1 : 3. The following table gives approximately the constant proportion for each sense :—

Tactile Sensation,	1 : 3.	$\frac{1}{3}$	Muscular Sensation,	6 : 100.	$\frac{6}{100}$
Thermal ,,	1 : 3.	$\frac{1}{3}$	Visual ,,	1 : 100.	$\frac{1}{100}$]
Auditory ,,	1 : 3.	$\frac{1}{3}$			

[The application of the law to temperature sensations is beset with great difficulties, while for taste and smell we do not know that it is really applicable. From an experimental point of view, it cannot be said to be proved, and its application is obviously somewhat restricted to certain sensations, and to these only within a certain range. It certainly does not hold good for sensations of pressure, and muscular sense, near the lower limits for these senses. "At best it is only an approximately correct statement of what holds true of the relative intensity of certain sensations of light and hearing, and less exactly of pressure and the muscular sense, when these sensations are of moderate strength" (*Ladd*).]

The term **after-sensation** is applied to the following phenomenon, viz., that, as a rule, the sensation lasts longer than the stimulus producing it; thus, there is an after-sensation after pressure is applied to the skin. **Subjective sensations** occur when stimuli due to internal somatic causes excite the nervous apparatus of the sense organ. The highest degrees of these, depending mostly upon pathological stimulation of the sensory cortical centres, are characterised as **hallucinations**, *e.g.*, when a delirious person imagines he sees figures or hears sounds which have no objective reality. In opposition to this condition the term **illusion** is applied to modifications by the sensorium of sensations actually caused by external objects, *e.g.*, when the rolling of a waggon is mistaken for thunder.

In a **new-born child** the sense of touch is strongly developed, that of pain slightly, muscular sensations are undoubtedly present, while smell and taste are frequently confounded. Auditory stimuli are heard from the second day onwards, the stimulus of light immediately after birth, but a peripheral field of vision does not yet exist (*Cuignet*). Towards the fourth to fifth week, the movements of convergence and accommodation are noticeable, while after four months colours are distinguished. The various stimuli are not perceived simultaneously—a reflex inhibitory centre is not yet developed (*Genzmer*).

The Visual Apparatus—The Eye.

384. HISTOLOGICAL OBSERVATIONS.—In the following remarks it is assumed that the student is familiar with the anatomical structure of the eye :—

The cornea, for the sake of simplicity, is regarded as uniformly spherical, although, properly speaking, it differs slightly from this form. It is more like a *vertical* section of a somewhat oblate ellipsoid, which we must suppose to be formed by rotating an ellipse around its long axis. It is nearly of uniform thickness throughout, only in the infant it is slightly thicker in the centre, and in the adult slightly thinner.

The **cornea** consists of the **following layers** :—

[1. Anterior stratified epithelium.
2. Anterior elastic lamina.
3. Substantia propria.
4. Posterior elastic lamina.
5. Single layer of epithelium.]

1. The **anterior epithelium**, stratified and nucleated, consists of many layers of cells (fig. 641, *a*). The deepest cells are more or less columnar, are arranged side

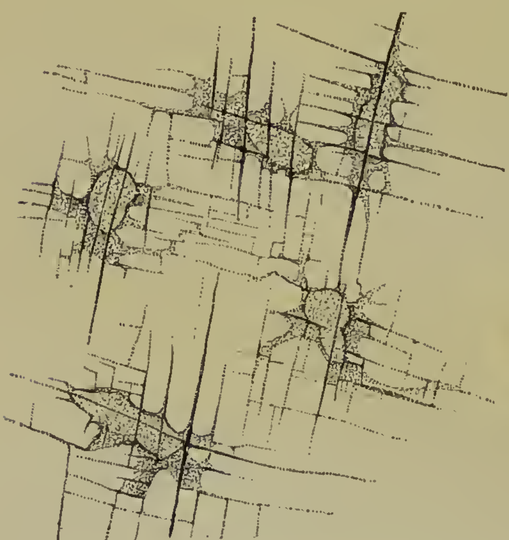


Fig. 639.

Fig. 640.

Fig. 639.—Cornea of the frog treated with chloride of gold, showing the corneal corpuscles stained, and a few nerve-fibrils. Fig. 640.—Cornea of the frog treated with silver nitrate ; the ground substance is stained, while the spaces for the corneal corpuscles are left unstained.

by side, and are called supporting cells. [Frequently nuclei divided by mitosis are to be seen, so that new cells are produced by proliferation of the deepest cells.] The cells of the middle layers are more arched, and dip with finger-shaped processes into corresponding spaces between their neighbours. The most superficial cells are flat, perfectly smooth, hard, keratin-containing squamous epithelium, [and in many respects resemble the squames of the mouth].

2. The epithelial layer rests upon the **anterior elastic membrane** (Bowman's elastic lamina), a structureless, clear, basement-like membrane (*b*). In man it is about 10 μ in thickness, but its thickness varies with the animal investigated.

3. The **substantia propria** of the cornea consists of (chondrin-yielding) fibres composed of delicate fibrils of connective-tissue. The fibres are arranged in mat-like thin **lamellæ** (*l*), more or less united together, and are placed in layers over each other. Towards the anterior elastic lamina, the fibres bend round and per-

forate the superficial lamellæ, thus serving as supporting fibres. [These perforating fibres are comparable to Sharpey's fibres in bone.] Between the lamellæ are a series of inter-communicating spaces lined by endothelium. These spaces are really **lymph-spaces**, and they communicate with the lymphatics of the conjunctiva. The fixed **corneal corpuscles** lie in these spaces (*c*), and are provided with numerous processes, which anastomose with the processes of corpuscles lying between the lamellæ above and below, and on either side of them. Kühne

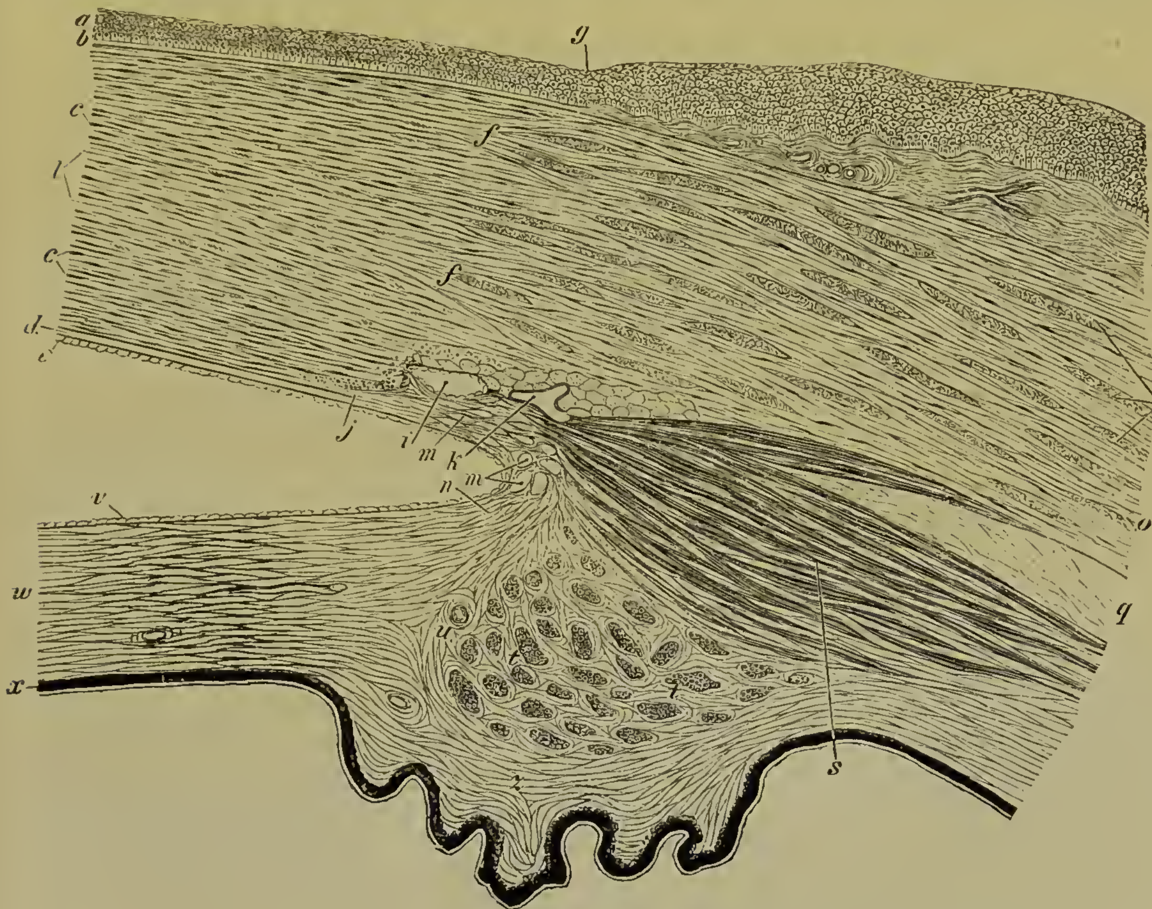


Fig. 641.

Antero-posterior section at the junction of the cornea with the sclerotic. *a*, anterior corneal epithelium ; *b*, Bowman's lamina ; *c*, corneal corpuscles ; *l*, corneal lamellæ (the whole thickness lying between *b* and *d* is the substantia propria corneæ) ; *d*, Descemet's membrane ; *e*, its epithelium ; *f*, junction of cornea with the sclerotic ; *g*, limbus conjunctivæ ; *h*, conjunctiva ; *i*, canal of Schlemm ; *k*, Leber's venous plexus (is regarded by Leber as belonging to *i*) ; *m*, *m*, meshes in the tissue of the lig. iridis pectinatum ; *n*, attachment of the iris ; *o*, longitudinal, *p*, circular (divided transversely) bundles of fibres of the sclerotic ; *q*, perichoroidal space ; *s*, meridional [radiating], *t*, equatorial (circular) bundles of the ciliary muscle ; *u*, transverse section of a ciliary artery ; *v*, epithelium of the iris (a continuation of that on the posterior surface of the cornea) ; *w*, substance of the iris ; *x*, pigment of the iris ; *z*, a ciliary process.

observed that stimulation of the corneal nerves was followed by contraction of these cells (§ 201, 7), while Kühne and Waldeyer maintain that they are connected with the corneal nerve-fibrils.

[The **corneal corpuscles** are looked upon as branched connective-tissue corpuscles lying in and not quite filling the branched spaces between the lamellæ. The processes anastomose freely with similar cells in the same plane, and to a less extent with the processes of cells in planes immediately above and below them. In a

section stained with gold chloride, they present the appearance seen in fig. 639. In a vertical section of the cornea they appear fusiform and parallel to the free surface of the cornea (fig. 641). If the cornea of a frog be pencilled with silver nitrate, the cement-substance between the lamellæ is blackened, and the branched cell-spaces remain clear, as in fig. 640. The one figure represents, as it were, the positive, and the other the negative image.] Leucocytes also pass into these lymph-spaces, or juice-canals. The importance of these leucocytes in inflammation is referred to in § 200.

[The lamellæ of the cornea in the Rays are traversed by "**sutural fibres**" which pass at right angles to the plane of the lamellæ from the anterior elastic lamina to Descemet's membrane (*Ranvier*).]

4. The transparent, structureless, **posterior elastic membrane** (*d*), the membrane of Descemet or Demours, is in many animals fibrillated, and shows evidence of stratification, while towards the margin of the cornea there are occasionally slight conical elevations. This membrane is very tough and very resistant (of great importance in inflammation). If it be removed, it rolls up towards the convex side. At its periphery it becomes continuous with the fibro-elastic reticulated ligamentum pectinatum iridis, whose trabeculæ are covered by epithelium.

5. The posterior **single layer of epithelium** consists of flat, delicate, nucleated cells (*e*), which are continued from the margin of the cornea on to the anterior surface of the iris (*v*). Fine juice-canals exist in the spaces between the individual cells (*v. Recklinghausen*). These spaces communicate with a system of fine tubes under the epithelium, perforate Descemet's membrane, and thus communicate with the corneal spaces.

[**Bowman's tubes** are artificial productions, formed by forcing air or a coloured fluid between the lamellæ, when it passes between the bundles of fibrils, forming a series of tubes with dilatations on them and running at right angles to one another between the lamellæ.]

The **nerves** of the **cornea**, which are derived from the **long** and **short ciliary nerves** (§ 347), are partly **sensory** in function. They enter the cornea at its margin as medullated fibres, but the myelin soon disappears, while the axial cylinders split up into fibrils. [The axial cylinders branch and form a plexus between the lamellæ, especially near the anterior surface, the **fundamental** or **ground plexus** (fig. 642, *n*). There are triangular nuclei at the nodal points, but they probably belong to the sheath of flattened cells which cover the larger branches. There is a finer and denser plexus of fibrils immediately under the anterior epithelium, **sub-epithelial plexus**, which is derived from the former, the fibrils arising in pencils or groups (fig. 643). Some fibrils perforate the anterior elastic lamina, **rami perforantes**, and pass between the anterior epithelial cells to form the **intra-epithelial network** (fig. 642, *b*, *p*). Some observers suppose that they terminate in free, pointed, or bulbous ends. There is also a fine plexus of

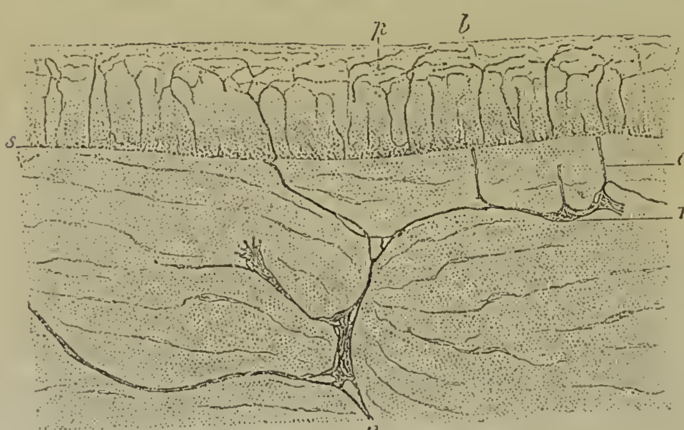


Fig. 642.

Vertical section of the cornea stained with gold chloride. *n*, nerve-fibrils; *a*, perforating branch; *r*, nucleus; *p*, *b*, inter-epithelial termination of fibrils; *s*, anterior elastic lamina.

fibrils in the posterior layers of the cornea, near Descemet's membrane. It gives off numerous fine fibrils, which come into intimate, if not direct, anatomical relation with the corneal corpuscles. The *trophic* fibres of the cornea (§ 347) are, perhaps, those deeper branches which are connected with the corneal corpuscles.

[**Method.**—These fibrils are best revealed by staining a cornea with chloride of gold, which tinges them of a purplish hue after exposure to light (*Cohnheim*). They are also readily stained by methylene blue.]

Blood-vessels occur only in the outer margin of the cornea (fig. 645, *v*), and extend 2 mm. over the cornea above, 1·5 mm. below, and 1 mm. laterally—the most external capillaries form arched loops, and thus turn on themselves. The cornea is nourished from the blood-vessels in its margin. Opacities of the cornea give rise to many forms of visual defects.

The sclerotic is a thick fibrous membrane, composed of, *p*, circular (equatorial) and, *o*, longitudinal (meridional) bundles of connective-tissue woven together (fig. 641). The spaces between the bundles contain colourless and pigmented connective-tissue corpuscles and also leucocytes. It is thickest posteriorly, thinner at the equator, while in front of this it again becomes thicker, owing to the insertion of the tendons of the straight muscles of the eyeball. It contains few blood-vessels, which form a wide-meshed capillary plexus, immediately under its deep surface. Other vessels form an arterial ring round the entrance of the optic nerve. It rarely is quite spherical; it rather resembles an ellipsoid, which we might imagine to be formed by the rotation of an ellipse around its short axis (short eyes) or around its long axis (long eyes). Above and below, the sclerotic overlaps like a fold the clear margin of the cornea; hence, when the cornea is viewed from before, it appears transversely elliptical; when seen from behind, it appears circular. Following the margin of the cornea, but lying still within the substance of the sclerotic, is the circular **canal of Schlemm** (*i*), which communicates with other anastomosing veins, the venous plexus of Leber (*k*). Schwalbe and Waldeyer regard Schlemm's canal as a lymphatic. Posteriorly, the sclerotic becomes continuous with the fibrous covering of the optic nerve derived from the dura mater. The sclerotic is provided with nerves, which are said to terminate in the cells of the scleral substance (*Helfreich*).

The **tunica uvea**, or the uveal tract, is composed of the choroid, the ciliary part of the choroid, and the iris.

The **choroid** is composed of the following layers (fig. 644):—(1) Most internally is the transparent **limiting membrane**, 0·7 μ in thickness, but it is slightly thicker anteriorly. (2) The very vascular capillary network of the **chorio-capillaris**, or membrane of Ruysch, embedded in a homogeneous layer. Then follows—(3) a layer of a thick **elastic network**, covered on both surfaces by endothelium (*Sattler*). (4) The **choroid proper** consists of a layer with pigmented connective-tissue corpuscles, together with a thick elastic network, containing the numerous venous vessels as well as the arteries. The pigmented layers are known as the **suprachoroidea**, or **lamina fusca**, which surrounds the large lymphatic space lined with endothelium and called the **perichoroidal space**, *q*. In new-born infants, which, according to Aristotle, have the iris dark blue, the uveal tissue is devoid of pigment; in brunettes it is developed later, and in blondes not at all.

In the **ciliary part** of the choroid, the pigmented connective-tissue corpuscles are not so numerous. The **ciliary muscle** (tensor choroideæ, or muscle of accommodation) is placed in this region. It arises (*s*) by means of a branched, reticulated, connective-tissue origin, from the inner side of the junction of the cornea and sclerotic, near the canal of Schlemm, and passes backwards to be inserted into the choroid. This constitutes the **radiating** fibres. Other fibres lying internal to these are arranged **circularly**, *t*, in bundles in the ciliary margin. These circular

fibres are sometimes called Heinrich Müller's muscle. The muscle consists of smooth muscular fibres, and is supplied by the oculomotorius (§ 345, 3).

The **iris** consists of the following parts from before backwards:—a layer of epithelial cells (*v*) continuous with those covering the posterior surface of the cornea, a layer of reticulated connective-tissue, the layer of blood-vessels, and lastly a posterior limiting membrane, which contains the pigmentary epithelium (*x*) (*Michel*). In brunettes, the texture of the iris contains pigmented connective-tissue corpuscles. The iris in some animals is described as containing two muscles composed of smooth muscular fibres—one set constituting the **sphincter pupillæ** (circular—fig. 660), which surrounds the pupil, and lies nearer the posterior than the anterior surface of the iris (§ 392). Its nerve of supply is derived from the oculomotorius (§ 345, 2). The other fibres constitute the **dilator pupillæ** (radiating), which consists of a thinner layer of fibres arranged in a radiate

Fig. 643.

Fig. 644.

Fig. 643.—Nerve-plexus in the cornea after gold chloride. *n*, nerve ; *a*, fibrils. Fig. 644.—Vertical section of the choroid and a part of the sclerotic. (1) sclerotic ; (2) lamina suprachoroidea ; (3) layer of large vessels ; (4) limiting layer ; (5) chorio-capillaris ; (6) hyaline membrane ; (7) pigment epithelium ; (*g*) large blood-vessels ; (*p*) pigment-cells ; (*c*) sections of capillaries.

manner. Some of the fibres reach to the margin of the pupil while others bend into the sphincter. [The existence of a dilator pupillæ in man is denied (§ 392).] At the outer margin of the iris, the radial bundles are arranged in anastomosing arches, and form a circular muscular layer (*Merkel*). The chief nerve of supply for the dilator fibres is the sympathetic (§ 347, 3). Ganglia occur in the ciliary nerves in the choroid, [and they are found also in the iris]. Gerlach has recently applied the term *ligamentum annulare bulbi* to that complex fibrous arrangement which surrounds the iris, and at the same time forms the point of union of the ciliary body, iris, ciliary muscle, sinus venosus iridis, and the line of junction of the cornea and sclerotic.

The **choroidal vessels** are of great importance in connection with the nutrition of the eye. According to Leber, they are arranged as follows:—The **arteries** are —1. The **short posterior ciliary**, which are about twenty in number, and perforate the sclerotic near the optic nerve (fig. 645 *a*, *a*). They terminate in the vascular network of the chorio-capillaris (*m*), which reaches as far as the ora serrata. 2.

The **long posterior ciliary**; one of these lies on the nasal and the other on the temporal side, and they run (*b*) to the ciliary part of the choroid, where they divide dichotomously, and penetrate into the iris, where they help to form the circulus arteriosus iridis major (*p*). 3. The **anterior ciliary** (*c*), which arise from the muscular branches, perforate the sclerotic anteriorly, and give branches to the ciliary part of the choroid and to the iris. About twelve branches run backwards (*o*) from them to the chorio-capillaris.

Veins of the Choroid.—1. The **anterior ciliary** veins (*c*) receive the blood from the anterior part of the uvea and carry it outwards. These branches are connected with Schlemm's canal and Leber's venous plexus. They do not receive any blood from the iris. 2. The **venous plexus** of the ciliary processes (*r*) receives the blood from the iris (*q*), and passes backwards to the choroidal veins. 3. The large **vasa vorticosa** (*h*) perforate the sclerotic behind the equator of the bulb.

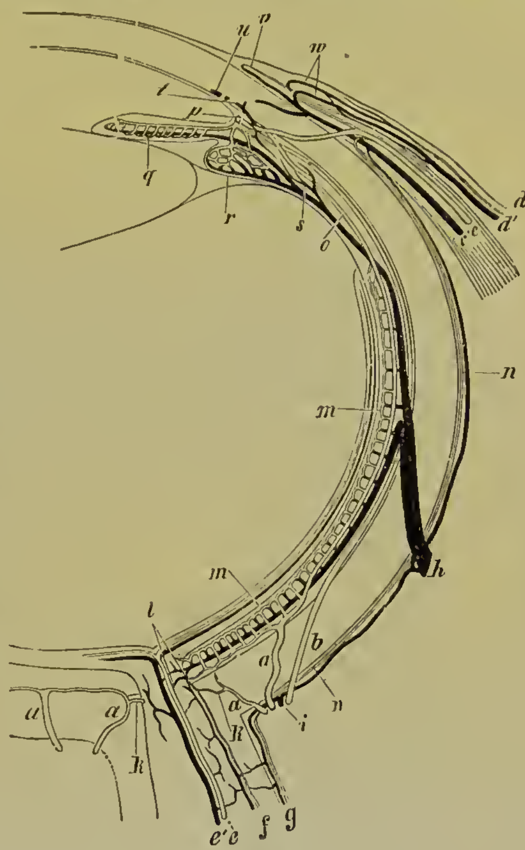


Fig. 645.

Diagram of the blood-vessels of the eye (horizontal view; veins black, arteries light, with a double contour). *a*, *a*, short posterior ciliary; *b*, long posterior ciliary; *c*, *c'*, anterior ciliary artery and vein; *d*, *d'*, artery and vein of the conjunctiva; *e*, *e'*, central artery and vein of retina; *f*, blood-vessels of the inner, and *g*, of the outer optic sheath; *h*, vorticose vein; *i*, posterior short ciliary vein confined to the sclerotic; *k*, branch of the posterior short ciliary artery to the optic nerve; *l*, anastomosis of the choroidal vessels with those of the optic; *m*, chorio-capillaris; *n*, episcleral branches; *o*, recurrent choroidal artery; *p*, great circular artery of iris (transverse section); *q*, blood-vessels of the iris; *r*, ciliary process; *s*, branch of a vorticose vein from the ciliary muscle; *t*, branch of the anterior ciliary vein to the ciliary muscle; *u*, circular vein; *v*, marginal loops of vessels on the cornea; *w*, anterior artery and vein of the conjunctiva.

The inner margin of the iris rests upon the anterior surface of the lens; the posterior chamber is small in adults, and in the new-born child it may be said scarcely to exist—it is so small. When Berlin blue is injected into the anterior chamber of the eye, it generally passes into the anterior ciliary veins (*Schwalbe*). Even in living animals, carmine also behaves in a similar manner (*Heisrath*); hence these observers conclude that there is a *direct* communication between the veins and the aqueous chamber, as these substances do not diffuse through membranes.

Internal to the choroid lies the single layer of **hexagonal cells** (0·0135 to 0·02 mm. in breadth) filled with crystalline pigment. This layer really belongs to the retina. It consists of a single layer of cells as far as the ora serrata—it is continued on to the ciliary processes and the posterior surface of the iris, where it forms several layers (fig. 641, *x*). In albinos it is devoid of pigment; on the other hand, the uppermost cells, which lie on the ridges of the ciliary processes, are always devoid of pigment. [The processes of these cells vary in length with the kind of light acting on the retina (§ 398).]

The **retina** externally is in contact with the layer of hexagonal pigment-cells

(*Pi*), which in its development and functions really belongs to the retina. The cells are not flat, but they send pigmented processes into the space between the ends of the rods. [Du Bois states that the processes are continuous with the cones.] In some animals (rabbit) the cells contain fatty granules and other substances (p. 914). The cells are larger and darker at the ora serrata (*Kühne*).

The **retina** is composed of the following **layers**, proceeding from without inwards :—

[1. Layer of pigment-cells.
2. Rods and cones.
3. *External limiting membrane.*
4. Outer nuclear layer.
5. Outer molecular (granular reticular or internuclear layer).
6. Inner nuclear layer.
7. Inner molecular (granular or reticular) layer.
8. Layer of nerve-cells (ganglionic) layer.
9. Layer of nerve-fibres.
10. *Internal limiting membrane.*

1. The **hexagonal pigment-cells** already described. 2. The layer of **rods** and **cones** (*St*) or **neuro-epithelium** of Schwalbe [*bacillary layer*, or the *visual cells*, or *visual epithelium* of Kühne] (fig. 647). These lie externally next the choroid, but they are absent at the entrance of the optic nerve. Then follows the **external limiting membrane** (*Le*), which is perforated by the bases of the rods and cones. 3. The **external nuclear layer** (*äu.K*) ; this and all the succeeding layers are called "brain layers" by Schwalbe. 4. The **external granular** (*äu.gr*), or inter-nuclear layer, which is perforated by the fibres which proceed inwards from the nuclei of 3 to reach 5, the nuclei of the **internal nuclear layer** (*inK*). The nuclei of this layer, which are connected by fibres with the rods and cones, are marked by transverse lines in the macula lutea (*Krause*, *Denissenko*). [The so-called nuclei of the internal nuclear layer are not all of the same nature. The innermost layer consists of branched multipolar nerve-cells, so-called "spongio-blasts," and from many, but not all of them, an axis-cylinder process proceeds to the optic nerve-fibre layer. The other nuclei chiefly belong to bipolar nerve-cells, which send off a central process which breaks up into fine branches in the internal reticular layer, while a peripheral process breaks up in the external reticular layer. These are also the nuclei of the radiating fibres of Müller.] 6. The finely granular **internal granular** layer (*in.gr*), [called also neuro-spongium] through which the fibres proceeding from the inner nuclear layer cannot be traced. It would seem as if these fibres break up into the finest fibrils, into which also the branched processes of the ganglionic cells of 7, the **ganglionic layer**, extend. [The cells are nervous ganglionic cells, arranged in a single layer, and they contain no pigment. Each cell gives off centrally an unbranched axis-cylinder process which becomes continuous with a fibre of the optic nerve, and several branched protoplasmic processes which run peripherally and form numerous branches in the inner reticular layer. According to v. Vintschgau, the processes of the ganglionic cells are connected with the fibres. 8. The next, or fibrous layer, consists of the **fibres of the optic nerve** (*o*), and most internally is the **internal limiting membrane** (*Li*). The fibres of the optic nerve are devoid of myelin and arranged in bundles which radiate from the entrance of the optic nerve toward the ora serrata]. According to W. Krause, there are 400,000 broad, and as many narrow, optic fibres, so that for every fibre there are 7 cones, about 100 rods, and 7 pigment-cells. The optic fibres are absent from the macula lutea, where, however, there are numerous ganglionic cells. Between the two homogeneous limiting membranes (*Le* and *Li*) lies the **connective-tissue substance** of the retina. It contains the perforating fibres, or **Müller's fibres**, which run in a radiate manner between the two membranes, and hold the various layers of the retina together. They begin by a wing-shaped expansion at the internal limiting membrane (*Rk*), and in their course out-

wards contain nuclei (*k*). They are absent at the yellow spot. The supporting tissue forms a network in all the layers, holes being left for the nervous portions (*Sg*). The inner segments of the rods and cones are also surrounded by a sustentacular substance. As the retina passes forward to the ora serrata, it becomes thinner and thinner, gradually becoming richer in connective-tissue ele-

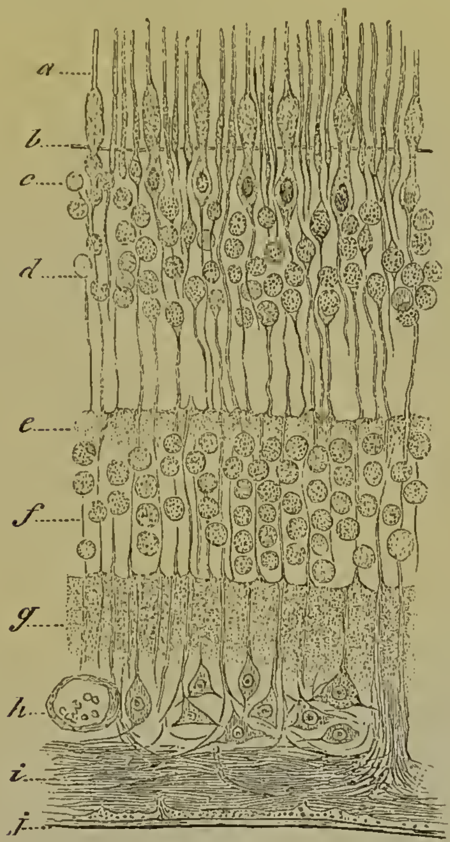


Fig. 646.

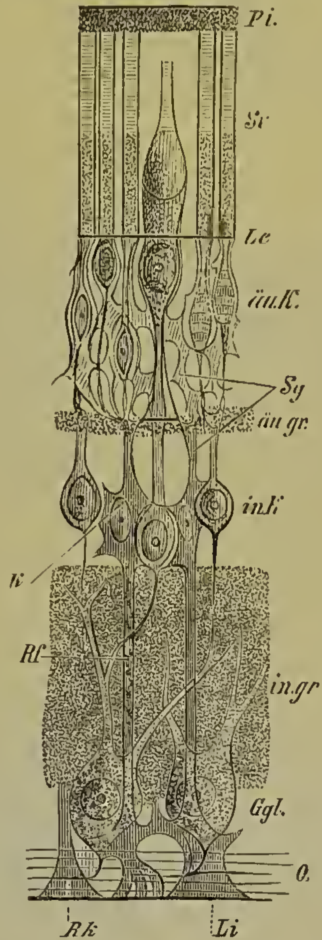


Fig. 647.

Fig. 646.—Vertical section of human retina. *a*, rods and cones; *b*, ext., and *j*, int. limit. memb.; *c*, ext., and *f*, int. nucl. layers; *e*, ext., and *g*, int. gran. layers; *h*, blood-vessel and nerve-cells; *i*, nerve-fibres. Fig. 647.—Layers of the retina. *Pi*, hexagonal pigment-cells; *St*, rods and cones; *Lc*, ext. limiting membrane; *äu.K.*, ext. nuclear layer; *äu.gr.* ext. granular layer; *inK.* int. nuclear; *in.gr*, int. granular; *Ggl*, ganglionic nerve-cells; *o*, fibres of optic nerve; *Li*, int. limit. membrane; *Rk*, fibres of Müller; *K*, nuclei; *Sg*, spaces for the nervous elements.

ments and poorer in nerve elements, until, in the ciliary part, only the cylindrical cells remain (fig. 646).

[Ranvier divides the layers of the retina into an inner or cerebral part in which the blood-vessels are distributed, and an outer layer—neuro-epithelial—which contains no blood-vessels. The following classification shows the difference:—

Table of the Layers of the Retina.

After Ranvier.	*Classical Classification.*
I. Neuro-epithelial part.	
Pigmentary layer.	Pigmentary layer.
Rods and cones.	Jacob's membrane.
External limiting membrane.	External limiting membrane.
Bodies of the visual cells, *i.e.*, rods and cones.	External nuclear layer.
Basal plexus. Basal cells.	External granular layer.

After Ranvier.	*Classical Classification.*
II. Cerebral part.	
Layer of unipolar nerve-cells. Layer of bipolar nerve-cells.	Internal nuclear layer.
Cerebral plexus.	Internal granular layer.
Multipolar nerve-cells.	Multipolar nerve-cells.
Fibres of the optic nerve.	Fibres of the optic nerve.
Internal limiting membrane.	Internal limiting membrane.]

[**Macula Lutea and Fovea Centralis.**—There are no rods in the fovea, cones only are present, and they are longer and narrower than in the other parts of the retina (fig. 648). The other layers also are thinner, especially at the macula lutea, but they become thicker towards the margins of the fovea, where the ganglionic layer consists of several rows of bipolar cells. The yellow tint is due to pigment lying between the layers composing the yellow spot.]

The **blood-vessels** of the retina lie in the *inner* layers near the inner granular layer. Only near the entrance of the optic nerve are they connected by fine branches with the choroidal vessels; they are surrounded by perivascular lymph-spaces. The greatest number of capillaries runs in the layers external to the inner granular layer (*Hesse*). The fovea centralis is devoid of blood-vessels (*Nettleship*, *Becker*). Except in mammals, the eel (*Denissenko*), and some tortoises (*H. Müller*), the retina receives no blood-vessels. Destruction of the retina is followed by blindness.

[**Retinal Epithelium.**—The single layer of pigmentary cells containing granules of a kind of melanin sends processes downwards, like the hairs of a brush, between the rods and cones (§ 398). Kühne has shown that the nature and amount of

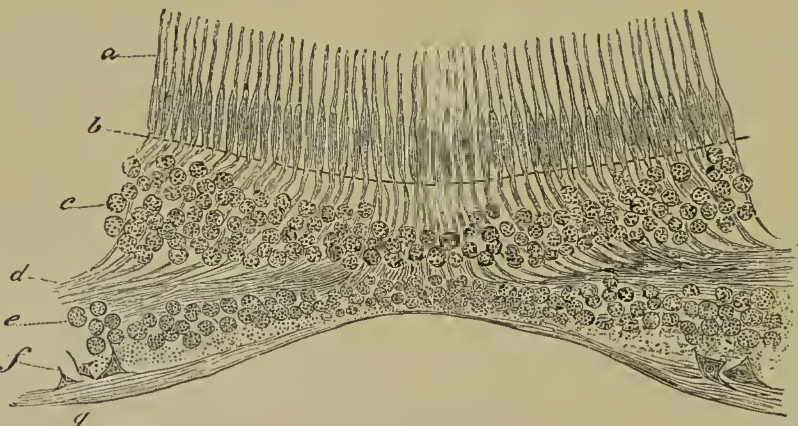


Fig. 648.

Section of the fovea centralis. *a*, cones; *b* and *g*, int. and ext. limit. memb.; *c*, ext., and *e*, nuclear layer; *d*, fibres; *f*, nerve-cells.

light influence the condition of these processes (fig. 693). The protoplasm of these cells in a frog kept for several hours in the dark is retracted, and the pigment-granules lie chiefly in the body of the cell and in the processes near the cell. In a frog kept in bright daylight, the processes loaded with pigment penetrate downwards between the rods and cones as far as the external limiting membrane.]

[The black variety of melanin found in the hexagonal cells of the retina is called **fuscin**. The outer part of each cell consists of neuro-keratin, but the inner part is loaded with granules of fuscin, and the cell-protoplasm exhibits movements like those of protoplasm under the influence of light. It is a nitrogenous pigment, but it is doubtful if it contains iron, and even if it is derived from hæmoglobin].

[**Tapetum.**—In the eye of the cat and dog a glancing iridescent appearance is seen in the retina. This is the tapetum which is due to many of the retinal

epithelial cells containing no fuscin. They, however, contain fine transparent crystals. In some fishes crystals of guanin occur, while the iridescent appearance of the tapetum in the eye of the ox and sheep is due to fibrous tissue.]

[Each **rod** and **cone** consists of an **outer** and an **inner segment**. During life, the outer segments of the rods contain a reddish pigment or the visual purple (*Boll*). Each rod is 60 μ long and 2 μ broad. The outer segment of each rod is doubly refractive and tends to split up into transverse discs. It is narrower than the inner segment and is stained black by osmic acid. The inner finely granular segment is stained by carmine, and often presents a striated appearance. At its outer part it contains an elliptical fibrous apparatus. The nucleus in the body of each rod lying in the external nuclear layer is marked by two or three transverse bands. The outer segment of the cones is shorter and more conical than that of the rods, while the inner segment is thick and bulging. The outer segment of each rod and cone consists externally of a membrane composed of neuro-keratin, containing a substance described by Kühne as myeloidin, which is the substance stained black by osmic acid, and it is perhaps a compound of lecithin and a globulin.]

Visual purple [or **rhodopsin**] may be preserved by keeping the eye in darkness; but it is soon bleached by daylight, while it is again restored when the eye is placed in darkness. It can be extracted from the retina by means of a 2·5 per cent. solution of the bile acids, especially from eyes that have been kept in 10 per cent. solution of common salt (*Ayres*) The rods are 0·04 to 0·06 mm. high and 0·0016 to 0·0018 mm. broad, and exhibit longitudinal striation, produced by the presence of fine grooves; a fine fibril runs in their interior (*Ritter*). The external segment occasionally cleaves transversely into a number of fine transparent discs. [It is a very resistant structure, and in this respect resembles neuro-keratin.] Krause found an ellipsoidal body, the "rod ellipsoid," at the junction at the inner and outer segments of the rods. The cones are devoid of visual purple, but their outer segment is striated longitudinally, and it also readily breaks across into thin discs. Only cones are present in the macula lutea. In the neighbourhood of the yellow spot, each cone is surrounded by a ring of rods. The cones become less numerous towards the periphery of the retina. In nocturnal animals, such as the owl and bat, there are either no cones or imperfect ones. The retinæ of birds contain many cones, that of the tortoise only cones. The rods and cones rest on the sieve-like perforated external limiting membrane (*Le*). Both send processes through the membrane, the cones to the larger and higher-placed nuclei, the rods to the nuclei, with transverse markings in the external nuclear layer. [The cones are particularly large in some fishes, *e.g.*, the cod, while the skate has no cones, but only rods. The same is the case in the shark and sturgeon, hedgehog, bat, and mole.]

[**Distribution and Regeneration of Rhodopsin.**—Keep a rabbit in the dark for some time, kill it, remove its eyeball, and examine its retina by the aid of monochromatic (sodium) light. The retina will be purple-red in colour, all except the macula lutea and a small part at the ora serrata. The pigment is confined to the *outer segments of the rods*. It is absent in pigeons, hens, and one bat, although the last has only rods. It is found both in nocturnal and diurnal animals. Its colour is quickly bleached by light, and it fades rapidly at a temperature of 50° to 76° C., while trypsin, alum, and ammonia do not affect it. It is restored in the retina by the action of the retinal epithelium. If the retinal epithelium or choroid be lifted off from an excised eye exposed to light, the purple is destroyed; but if the eye be placed in darkness and the retinal epithelium replaced, the colour is restored.]

Chemistry of the retina.—The reaction of the retina, when quite fresh, is acid, and becomes alkaline in darkness. The rods and cones contain albumin, neuro-keratin, nuclein, and in the cones are the pigmented oil-globules, the so-called "**chromophanes**." The other layers contain the constituents of the grey matter of the brain.

[**Chromophanes, the pigments of the Cones.**—There is no colouring matter in the outer segment of the cones, but in fishes, reptiles, and birds the inner segment contains a globular or coloured body, often red and yellow, the pigment being held in solution by a fatty body. Kühne has separated a green (**chlorophane**), a yellow (**xanthophane**), and a red (**rhodophane**) pigment. They all give a blue with iodine, and are bleached by light (*Schwalbe*).]

The crystalline lens is enclosed in a transparent **capsule**, thicker anteriorly than posteriorly, and it is covered on the inner surface of the anterior wall by a layer of low epithelium. Towards the margin of the lens, these cells elongate into nucleated fibres, which all bend round the margin of the lens, and on both sides of the lens abut with their ends against each of the triradiate figures. The lens fibres contain globulin enclosed in a kind of membrane. Owing to mutual pressure, they are hexagonal when seen in transverse section (fig. 649, 2), while in many animals, especially fishes, their margins are serrated, and the teeth dovetail into each other. For the sake of simplicity, we may regard the lens as a biconvex body with spherical surfaces, the posterior surface being more curved. As a matter of fact, the anterior part is part of an ellipsoid formed by rotation on its short axis. The posterior surface resembles the section of a paraboloid, *i.e.*, we might regard it as formed by the rotation of a parabola on its axis (*Brücke*). The outer layers of the lens have less refractive power than the more internal layers. The central part of the lens or nucleus is, at the same time, firmer, and more convex than the entire lens. The margin of the lens is always separated from the ciliary processes by an intermediate space.

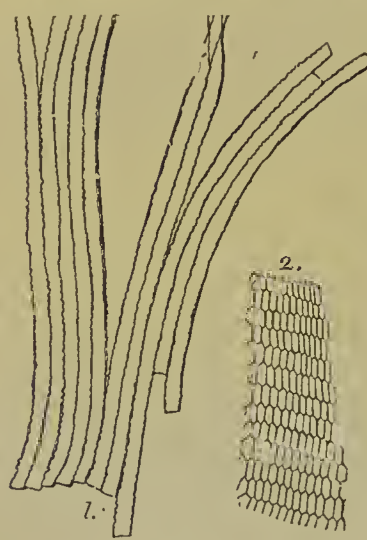


Fig. 649.
1, Fibres of the lens ; 2, transverse sections of the lens fibres.

[**Chemistry of the lens.**—The lens contains about two-thirds of its weight of water (63·50 per cent.), while its chief solid is a globulin, called by Berzelius **crystallin** (24·6 per cent.), salts, cholesterin, and fats. Albumin is said to be absent, but it is present in the ox lens.]

[**Cataract.**—Sometimes the lens becomes more or less opaque, the opacity beginning either in the middle or outer parts of the lens. This is generally due to fatty degeneration of the fibres, cholesterin being deposited. An opaque, cataractous condition of the lens may be produced in frogs by injecting a solution of some salts or sugar into the lymph-sacs; the result is that these salts absorb the water from the lens, and thus make it opaque. The cataract of diabetes is probably produced from the presence of grape-sugar in the blood.]

The **zonule of Zinn**, at the ora serrata, is applied as a folded membrane to the ciliary part of the uvea, so that the ciliary processes are pressed into its folds, and are united to it. It passes to the margins of the lens, where it is inserted by a series of folds into the anterior part of the capsule of the lens. Behind the zonule of Zinn, and reaching as far as the vitreous humour, is the **canal of Petit.** The zonule is a fibrous perforated membrane. According to Merkel, the canal of Petit is enclosed by very fine fibres, so that it is really not a canal but a complex communicating system of spaces (*Gerlach*). Nevertheless, the zonule represents a stretched membrane, holding the lens in position, and may therefore be regarded as the **suspensory ligament** of the lens.

Opacity or cloudiness of the lens (grey cataract) hinders the passage of light into the eye. Aphakia, or the absence of the lens (as after operations for cataract), may be remedied by a pair of strong convex spectacles. Of course, such an eye does not possess the power of accommodation.

The vitreous humour, so far as the ora serrata, is bounded by the internal limiting membrane of the retina (*Henle*, *Iwanoff*). From here forwards, lying between both, are the meridional fibres of the zonule, which are united with the surface of the vitreous and the ciliary processes. A part of the fibrous layer bends into the saucer-shaped depression and bounds it. A canal, 2 mm. in diameter, runs from the optic papilla to the posterior surface of the capsule of the lens; it is called the **hyaloid canal**, and was formerly traversed by blood-vessels. The peripheral part of the vitreous humour is laminated like an onion, the middle is homogeneous; in the former, especially in the fœtus, are round fusiform or branched cells of the mucous tissue of the vitreous, while in the centre there are disintegrated remains of these cells (*Iwanoff*). The vitreous humour contains a very small percentage of solids, 1·5 per cent. of **mucin**, [and according to Pickard, there is 0·5 per cent. of urea, and about ·75 of sodic chloride].

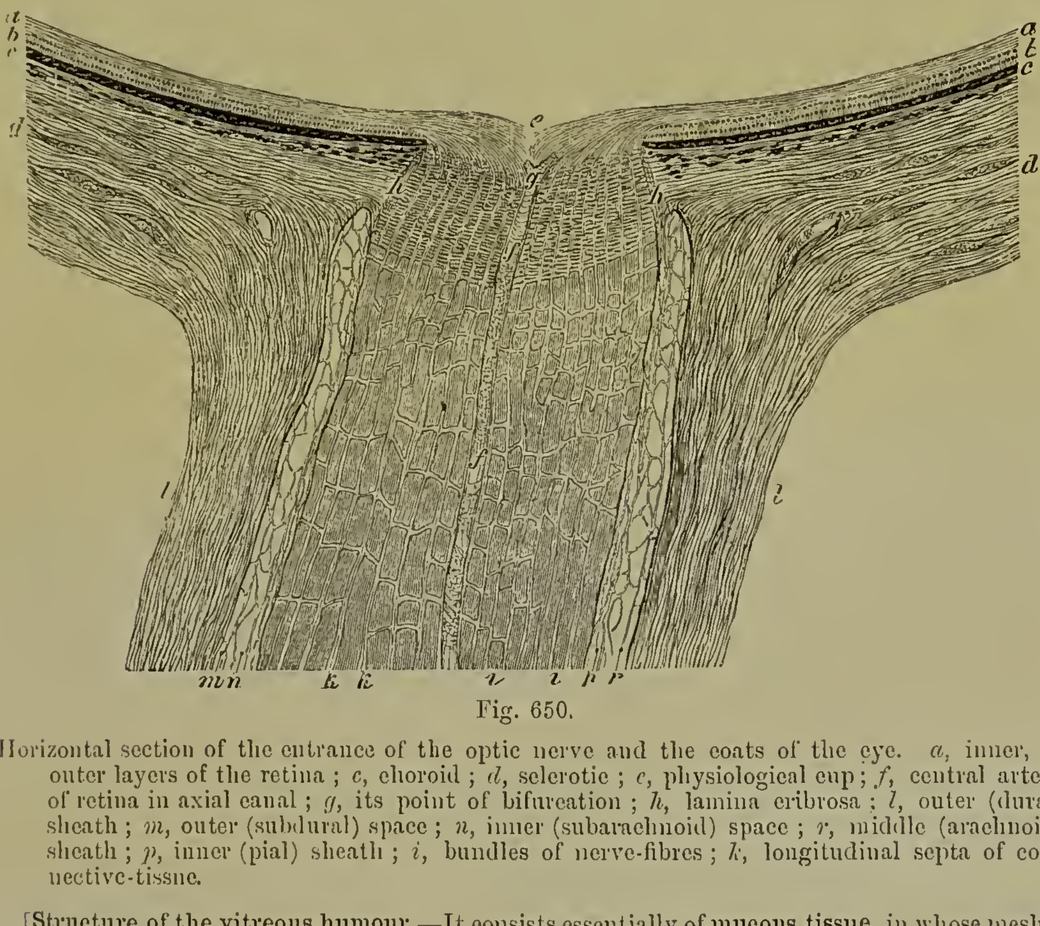


Fig. 650.

Horizontal section of the entrance of the optic nerve and the coats of the eye. *a*, inner, *b*, outer layers of the retina; *c*, choroid; *d*, sclerotic; *e*, physiological cup; *f*, central artery of retina in axial canal; *g*, its point of bifurcation; *h*, lamina cribrosa; *l*, outer (dural) sheath; *m*, outer (subdural) space; *n*, inner (subarachnoid) space; *r*, middle (arachnoid) sheath; *p*, inner (pial) sheath; *i*, bundles of nerve-fibres; *k*, longitudinal septa of connective-tissue.

[**Structure of the vitreous humour.**—It consists essentially of **mucous tissue**, in whose meshes lies a very watery fluid, containing the organic and inorganic bodies in solution. It contains 1·1 per cent. of solids, including a trace of albumin, a mucoid body, a trace of urea, and salts. According to Younan, the vitreous contains two types of cells—(1) **amœboid cells** of various shapes and sizes. They lie on the inner surface of the lining hyaloid membrane and the other membranes in the cortex of the vitreous; (2) large **branching cells**. The vitreous is permeated by a large number of transparent, clear, homogeneous **hyaloid membranes**, which are so disposed as to give rise to a concentric lamination. The **canal of Stilling** represents in the adult the situation of the hyaloid artery of the fœtus. It can readily be injected by a coloured fluid.]

The **lymphatics** of the eye consist of an anterior and a posterior set. The **anterior system** consists of the anterior and posterior chambers of the eye (aqueous), which communicate with the lymphatics of the iris, ciliary processes, cornea, and conjunctiva. The **posterior** consist of the perichoroidal space between the sclerotic

and the choroid (*Schwalbe*). This space is connected by means of the perivascular lymphatics around the trunks of the vasa vorticosa, with the large lymph-space of Tenon, which lies between the sclerotic and Tenon's capsule. Posteriorly, this is continued into a lymph-channel, which invests the surface of the optic nerve; while anteriorly it communicates directly with the sub-conjunctival lymph-spaces of the eyeball. The optic nerve has **three sheaths**—(1) the **dural**; (2) the **arachnoid**; and (3) the **pial** sheath, derived from the corresponding membranes of the brain. **Two lymph-spaces** lie between these three sheaths—the **subdural space** between 1 and 2, and the **subarachnoid space** between 2 and 3 (fig. 636). Both spaces are lined by endothelium; and the fine trabeculæ passing from one wall to the other are similarly covered. According to Axel Key and Retzius, these lymph-spaces communicate anteriorly with the perichoroidal space.

The **aqueous humour** closely resembles the cerebro-spinal fluid, and contains albumin [and a reducing body, which is not sugar]; the former is increased, and the latter disappears after death. The same occurs in the vitreous. The albumin increases when the difference between the blood-pressure and the intra-ocular pressure rises. Such variations of pressure, and also intense stimuli applied to the eye, cause the production of fibrin in the anterior chamber (*Jesner and Grunhagen*). [It is a clear alkaline fluid, specific gravity 1003-1009, and containing 1·3 per cent. of solids, the proportion of proteids being only ·12 per cent. It is lymph, containing a very small quantity of solids, the chief inorganic solid being sodic chloride. The proteids are fibrinogen, serum-albumin, and serum-globulin. Traces of urea and sarco-lactic acid are present. The reducing substance does not undergo the alcoholic fermentation, and is therefore not sugar.]

Intraocular Pressure.—The cavity of the bulb is practically filled with watery fluids, which, during life, are constantly subjected to a certain pressure, the "intraocular pressure." Ultimately, this depends upon the blood-pressure within the arteries of the retina and uvea, and must rise and fall with it. The pressure is determined by pressing upon the eyeball, and ascertaining whether it is tense, or soft and compressible.

Just as in the case of the arterial pressure, the intraocular pressure is influenced by many circumstances; it is increased at every pulse-beat and at every expiration, while it is decreased during inspiration. The elastic tension of the sclerotic and cornea regulates the increase of the arterial pressure by acting like the air-chamber in a fire-engine; thus, when more arterial blood is pumped into the eyeball, more venous blood is also expelled. The constancy of the intraocular pressure is also influenced by the fact that, just as the aqueous humour is removed, it is secreted, or rather formed, as rapidly as it is absorbed (§ 392). [Fick has invented an instrument for the direct measurement of the intraocular pressure, a small plate of known size is pressed against the eyeball, and the pressure exerted is registered by means of a spring and index.]

The secretion of the aqueous humour occurs pretty rapidly, as may be surmised from the fact that hæmoglobin is found in the aqueous humour half an hour after dissolved blood (lamb's) is injected into the blood-vessels of a dog. It is rapidly reformed, after evacuation through a wound in the cornea.

According to Knies, the watery fluid within the eyeball is secreted, especially from the chorio-capillaris, and reaches the suprachoroidal space, in the lymph-sheaths of the optic nerve, and partly through the network of the sclerotic. It saturates the retina, vitreous humour, lens, and for the most part passes through the zonula ciliaris into the posterior chamber, and through the pupil into the anterior chamber. The movements of the fluid within the eyeball have been recently studied by Ehrlich, who used **fluorescin**, an indifferent substance, which, on being introduced into the body, passes into the fluids of the eyeball, and in a very dilute solution may be recognised by its green fluorescence in reflected light. From observations on the entrance of this substance into the eye, Schöler and Uhthoff regard the posterior surface of the iris and the ciliary body as the secretory organs for the aqueous humour. It passes through the pupil into the anterior chamber; some passes into the lens, and along the canal of Petit into the vitreous humour (*Pflüger*). Section of the cervical sympathetic, and still more of the trigeminus, accelerates the secretion of the aqueous, but its amount is diminished. If the substance is dropped into the conjunctival sac, it percolates towards the centre of the cornea, and through the latter into the anterior chamber (*Pflüger*).

A current passes forwards from the vitreous humour around the lens, and there is an outflow

along the central artery of the retina backwards through the optic nerve to the cavity of the skull (*Gifford*). The current in the spaces between the sheaths flows from the brain to the eye (*Quincke*).

The outflow of the aqueous humour, according to Leber and Heisrath, takes place chiefly between the meshes of the ligamentum pectinatum iridis (fig. 645, *m*, *m*), and the canal of Schlemm (*i*, *k*), into the anterior circular veins (p. 909). A small part of the aqueous humour diffuses into the posterior layers of the cornea, to nourish it (*Leber*). None of the water is conducted from the eyeball by any special efferent lymphatics (*Leber*). Under normal circumstances, the pressure is nearly the same in the vitreous and aqueous chambers, but atropin seems to diminish the pressure in the former and to increase it in the latter, whilst Calabar bean has an opposite action (*Ad. Weber*). Arrest of the outflow of the venous blood often increases the pressure in the vitreous, and diminishes that in the aqueous chamber. Compression of the bulb from without causes more fluid to pass out of the eye temporarily than enters it. The diminution of the intraocular pressure is well marked after section of the trigeminus, while it rises when this nerve is stimulated. The statements of observers regarding the effect of the sympathetic nerve upon the pressure vary. Interruption to the venous outflow increases the pressure, while an imperfect supply of blood, the outflow being normal, diminishes the pressure. The innervation of the blood-vessels of the eye is referred to at § 347.

385. **DIOPTRIC OBSERVATIONS.**—The **eye as an optical instrument** is comparable to a **camera obscura**; in both, an **inverted diminished image** of the

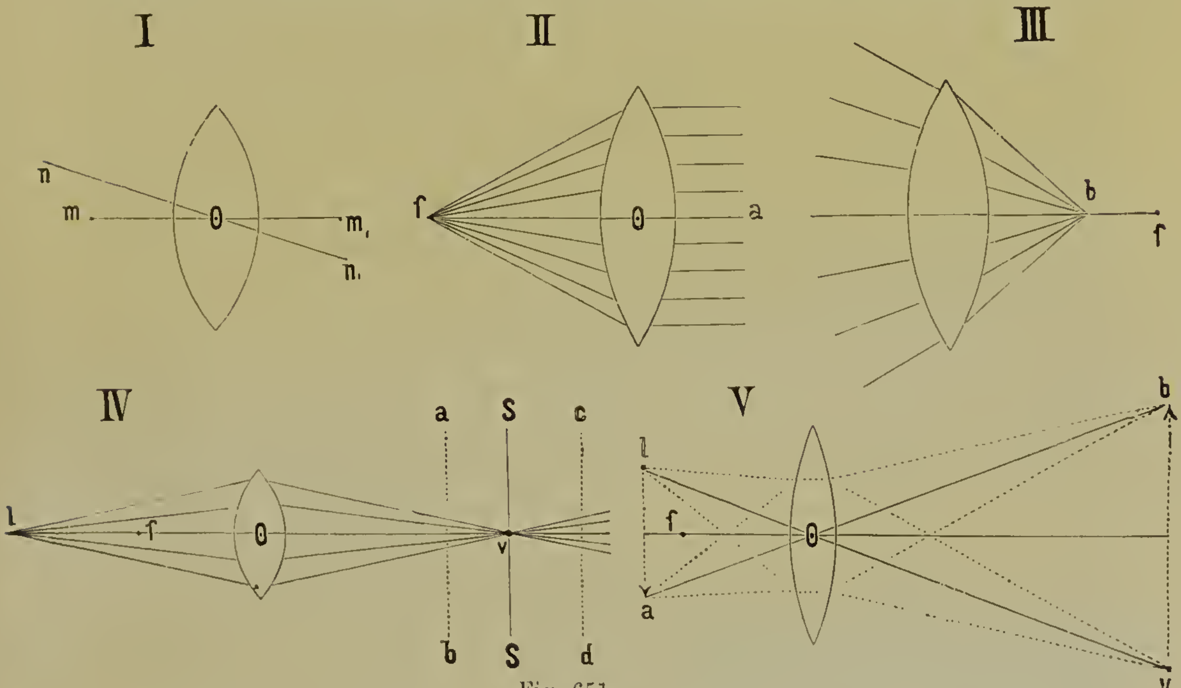


Fig. 651.

Figures illustrating the action of lenses upon rays of light passing through them.

objects of the external world is formed upon a background, the field of projection. Instead of the single lens of the camera, however, the eye has **several refractive media** placed behind each other—**cornea, aqueous humour, lens** (whose individual parts—capsule, cortical layers, and nucleus, all possess different refractive indices), and **vitreous humour**. Every two of these adjacent media are bounded by a "**refractive surface,**" which may be regarded as spherical. The field of projection of the eye is the retina, which is coloured with the visual purple (*Boll*, *Kühne*). As this substance is bleached chemically by the direct action of light, so that the pictures may be temporarily fixed upon the retina, the comparison of the eye with the camera of the photographer becomes more striking. In order that the passage of the rays of light through the media of the eye may be rightly understood, we must know the following factors:—(1) the refractive indices of all the media;

(2) the form of the refractive surfaces; (3) the distance of the various media from each other and from the field of projection or retina.

Action of a converging lens.—We must know how a convex lens acts upon light. In a convex lens we distinguish the centre of curvature, *i.e.*, the centre of both spherical surfaces (fig. 651, I, m, m_1). The line connecting both is called the **chief axis**; the centre of this line is the **optical centre** of the lens (o). All rays which pass through the optical centre of the lens pass through unbent, or without being refracted; they are called the chief or principal rays (n, n_1). The following are the laws regulating the action of a convex lens upon rays of light:—

1. Rays which fall upon the lens, **parallel** with the principal axis (II, f, a), are so refracted that they are collected on the other side of the lens, at a point called the focus or **principal focus** (f). The distance of this point from the central point (o) of the lens, is called the **focal distance** of the lens (f, o). The converse of this condition is evident, viz., rays which diverge from a focus and reach the lens, pass through it to the other side, parallel with the principal axis, without again coming together.

2. Rays of light proceeding from a source of light (IV, l) in the prolonged principal axis, but *beyond* the focal point (f), again converge to a point on the other side of the lens. The following cases may occur:—(a) When the distance of the light from the lens is equal to twice the focal distance, the focus or point of convergence lies at the same distance on the other side of the lens, *i.e.*, twice the focal distance. (b) If the luminous point be moved nearer to the focus, then the focal point is moved farther away. (c) If the light is still farther from the lens than twice the focal distance, then the focal point comes correspondingly near to the lens.

3. Rays proceeding from a point of the chief axis (III, b) within the focal distance, pass out at the other side less divergent, but do not come to a focus again. Conversely, rays which are convergent, and pass through a collecting lens, have their focal point within the focal distance.

4. If the luminous point (V, a) is placed in the secondary ray (a, b), the same laws obtain, provided the angle formed by the secondary ray with the principal axis is small.

Formation of images by convex lenses.—After what has been stated regarding the position of the point of convergence of rays proceeding from a luminous point, the construction of the image of any object by a convex lens is easily accomplished. This is done simply by projecting images of the various parts of the object. Thus, evidently (in V), b is the focal point of the object a, while v is the focal point of the object l. The picture is **inverted**. *Collecting lenses form an inverted and real image* (*i.e.*, upon a screen) *only of such objects as are placed beyond the focal point of the lens.*

With regard to the **size** and **distance** of the image from the lens, there are the following cases:—(a) If the object be placed at twice the focal distance from the lens, the image of the

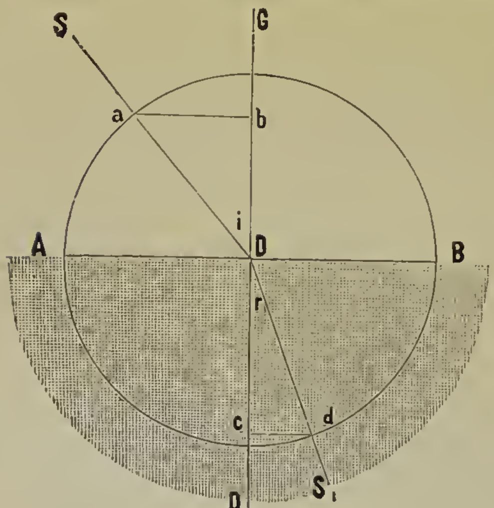


Fig. 652.

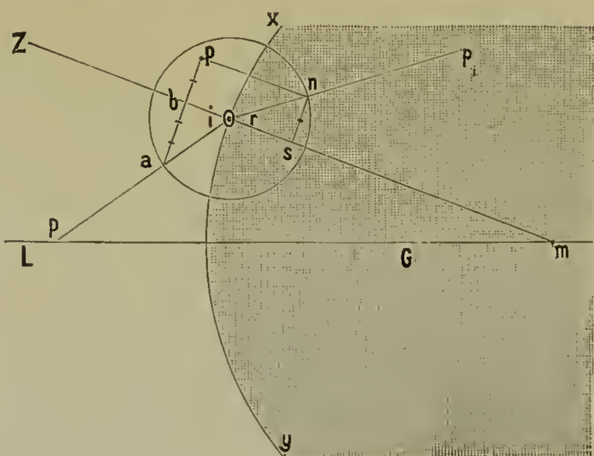


Fig. 653.

same is just the same size and at the same distance from the lens as the object is. (b) If the object be nearer than the focus, the image recedes and at the same time becomes larger. (c) If the object be farther removed from the lens than twice the focal distance, then the image is nearer to the lens and at the same time becomes smaller.

Position of the focal point.—The distance of the focal point from the lens is readily calculated according to the following formula:—Where l = the distance of the luminous point, b = the distance of the image, and f = the focal distance of the lens: $\frac{1}{l}+\frac{1}{b}=\frac{1}{f}$, or $\frac{1}{b}=\frac{1}{f}-\frac{1}{l}$.

Example.—Let $l=24$ centimetres, $f=6$ cm. Then $\frac{1}{b}=\frac{1}{6}-\frac{1}{24}=\frac{1}{8}$; so that $b=8$ cm., *i.e.*, the image is formed 8 cm. behind the lens. Further, let $l=10$ cm., $f=5$ cm. (*i.e.*, $l=2f$). Then $\frac{1}{b}=\frac{1}{5}-\frac{1}{10}=\frac{1}{10}$; so that $b=10$, *i.e.*, the image is placed at twice the focal distance of the lens. Lastly, let $l=\infty$. Then $\frac{1}{b}=\frac{1}{f}-\frac{1}{\infty}$; so that $b=f$, *i.e.*, the image of parallel rays coming from infinity lies in the focal point of the lens.

Refractive Indices.—A ray of light, which passes in a perpendicular direction from one medium into another medium of *different* density, passes through the latter without changing its course or being refracted. In fig. 652, if G D is $\perp$ A B, then so is D D $\perp$ A B; for a plane surface A B is the horizontal, and G D the vertical line. If the surface be spherical, then the vertical line is the prolonged radius of this sphere. If, however, the ray of light fall *obliquely* upon the surface, it is "**refracted**," *i.e.*, it is bent out of its original course. The incident and the refracted ray nevertheless lie in *one plane*. When the oblique incident ray passes from a *less dense* medium (*e.g.*, air) into one *more dense* (*e.g.*, water), the refracted or excident ray is bent *towards* the perpendicular. If, conversely, it pass from a more dense to a less dense medium, it is bent *away from* the perpendicular. The angle (i G D S) which the incident ray (S D) forms with the perpendicular (G D) is called the **angle of incidence**, the angle formed by the refracted ray (D S_1) with the prolonged perpendicular (D D) is called the **angle of refraction**, D D S_1 (r). The refractive power is expressed as the **refractive index**. The term **refractive index** (n) means that number which shows for a certain substance how many times the sine of the angle of incidence is greater than the sine of the angle of refraction, when a ray of light passes from the air into that substance. Thus, $n=\sin. i : \sin. r=ab : cd$. On comparing the refractive indices of two media, we always assume that the ray passes from *air* into the medium. On passing from the air into water, the ray of light is so refracted that the sine of the angle of incidence is to the sine of the angle of refraction as 4 : 3; the refractive index $\frac{4}{3}$ (or more exactly $=1{\cdot}336$). With glass the proportion is $=3:2=1{\cdot}535$—*Snellius*, 1620; *Descartes*). The sine of the incident and refractive angles are related as the velocity of light with both media.

The construction of the refracted ray, the refractive index being given, is simple :—**Example**—Suppose in fig. 653, L = the air, G = a dense medium (glass) with a spherical surface, xy, and with its centre at m; po = the oblique incident ray; mZ is the perpendicular; the $\angle\ i$ = the angle of incidence. The refractive index given is $\frac{3}{2}$; the object is to find the direction of the refracted ray. From o as centre describe a circle with a radius of any length; from a draw a perpendicular, $a\ b$ to $m\ Z$; then $a\ b$ is the sine of the angle of incidence, i. Divide the line $a\ b$ into three equal parts, and prolong it to the extent of two of these parts, viz., to p. Draw the line p parallel to mZ. The line joining o to n is the direction of the refracted ray. On making a line, $n\ s$, perpendicular to $m\ Z$, $n\ s=b\ p$. Further, $n\ s$ = sine $\angle\ =r$. So that $a\ b : s\ n$ or $: b\ p) = 3 : 2$ or $\sin. i : \sin. r=\frac{3}{2}$.

Optical cardinal point of a simple collecting system.—Two refractive media (fig. 654, L and G), which are separated from each other by a spherical surface (a, b), form a simple collecting system. It is easy to estimate the construction of an incident ray coming from the first medium (L) and falling obliquely upon the surface (a, b) separating the two media, as well as to ascertain its direction in the second medium, G, and also from the position of a luminous point in the first medium, to estimate the position of the corresponding focal point in the second medium. The factors required to be known are the following :—L (fig. 654) is the first, and G the second medium, a, b = the spherical surface whose centre is m. Of course, all the radii drawn from m to $a\ b$ ($m\ x$, $m\ n$) are perpendiculars, so that all rays falling in the direction of the radii must pass unrefracted through m. All rays of this sort are called **rays or lines of direction**; m, as the point of intersection of all these, is called the **nodal point**. The line which connects m with the vertex of the spherical surface, x, and which is prolonged in both directions, is called the **optic axis**, O Q. A plane (E, F) in x, perpendicular to O Q, is called the **principal plane**, and in it x is the **principal point**. The following facts have been ascertained :—(1) All rays (a to a_5), which in the first medium are parallel with each other and with the optic axis and fall upon $a\ b$, are so refracted in the second medium that they are all again united in one point (p_1) of the second medium. This is called the *second principal focus*. A plane in this point perpendicular to O Q is called the *second focal plane* (C D). (2) All rays (c to c_2), which in the first medium are parallel to each other, but not parallel to O Q, reunite in a point of the second focal plane (r), where the non-refracted directive ray (c_1, $m\ r$) meets this. (In this case, the angle formed by the rays c to c_2 with C Q must be very small.) The propositions 1 and 2 of course may be reversed; the divergent rays proceeding from p towards $a\ b$ pass into the first medium parallel to each other, and also with the axis C Q (a to a_5); and

the rays proceeding from r pass into the first medium parallel to each other, but not parallel to the axis O Q (as c to c_2). (3) All rays, which in the second medium are parallel to each other (b to b_5) and with the axis O Q, reunite in a point in the first medium (p) called the *first focal point*; of course the converse of this is true. A plane in this point perpendicular to O Q is called the *first focal plane* (A, B). The radius of the refractive surface (m, x) is equal to the

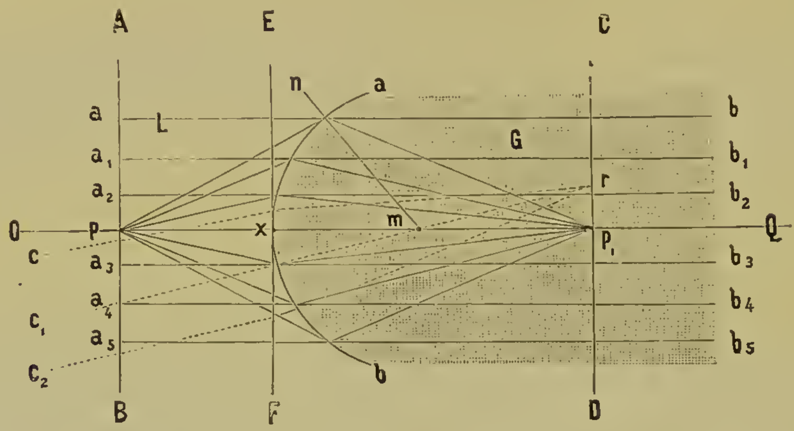


Fig. 654.

difference of the distance of both focal points (p and p_1) from the principal focus (x); thus $m\,x = p_1\,x\;p\,x$. From these comparatively simple propositions it is easy to determine the following points:—

1. **The construction of the refracted ray.**—Let A be the first (fig. 655); B, the second medium; c d, the spherical surface separating the two; a b, the optical axis; k, the nodal point; p, the first and p_1 the second principal focus; C, D, the second focal plane. Suppose x y to represent the direction of the incident ray, what is the construction of the refracted ray in the second medium? Prolong the unrefracted ray, P k, to Q parallel to x y, then y Q is the direction of the refracted ray (according to 2).

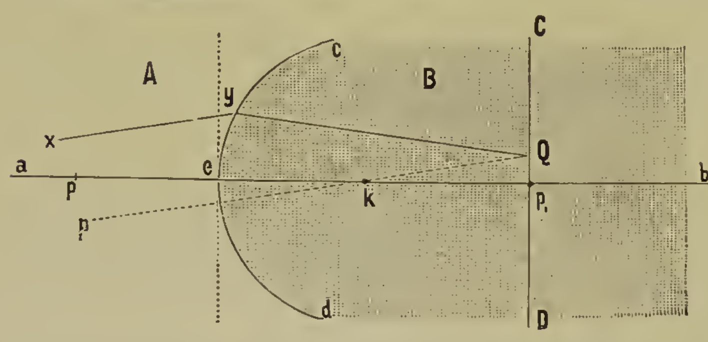


Fig. 655.

2. **Construction of the image for a given object.**—In fig. 656, B, c, d, a, b, k, p, and p_1, C, D are as before. Suppose a luminous point (o) in the first medium, what is the position of the image in the second medium? Prolong the unrefracted ray (o, k, P), and draw the ray (o, x) parallel to the axis (a, b). The parallel rays (a, c and o, x) reunite in p (according to pro-

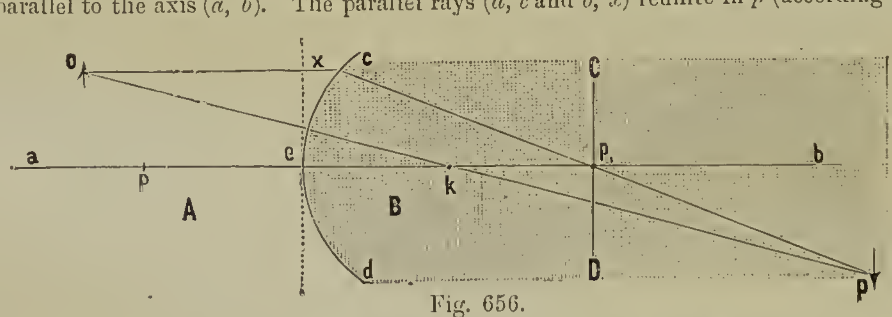


Fig. 656.

position 1). Prolong x, p_1 until it intersects the ray (o, P), then the image of o is at P—that is, the rays of light (o x and o k) proceeding from the luminous point (o) reunite in P.

Construction of the refracted ray and the image in several refractive media.—If several refractive media be placed behind each other, we must proceed from medium to medium with the same methods as above described. This would be very tedious, especially when dealing

with small objects. Gauss (1840) calculated that in such cases the method of construction is very simple. If the several media are "centred," *i.e.*, if all have the same optic axis, then the refractive indices of such a centred system may be represented by two equal, strong, refractive surfaces at a certain distance. The rays falling upon the first surface are not refracted by it, but are essentially projected forwards parallel with themselves to the second surface. Refraction takes place first at the second surface, just as if only *one* refractive surface was present. In order to make the calculation, we must know the refractive indices of the media, the radii of the refractive surfaces, and the distance of the refractive surfaces from each other.

Construction of the refracted ray is accomplished as follows :—Let $a\ b$ represent the optical axis (fig. 657, I.) ; H, the first focal point determined by calculation ; $h\ h$, the principal plane ; H, the second focal point ; h_1, h_1, the second principal plane ; k, the first, and k_1 the second nodal point ; F, the second focal point ; and F_1, F_1, the second focal plane. Make the ray of direction $p\ k_1$ parallel to m_1, n_1. According to proposition 2, p, k_1 and m_1, n_1 must meet in a point of the plane F_1 F_1. As $p\ k_1$ passes through unrefracted, the ray from n_1 must fall at r ; $n_1\ r$ is, therefore, the direction of the refracted ray.

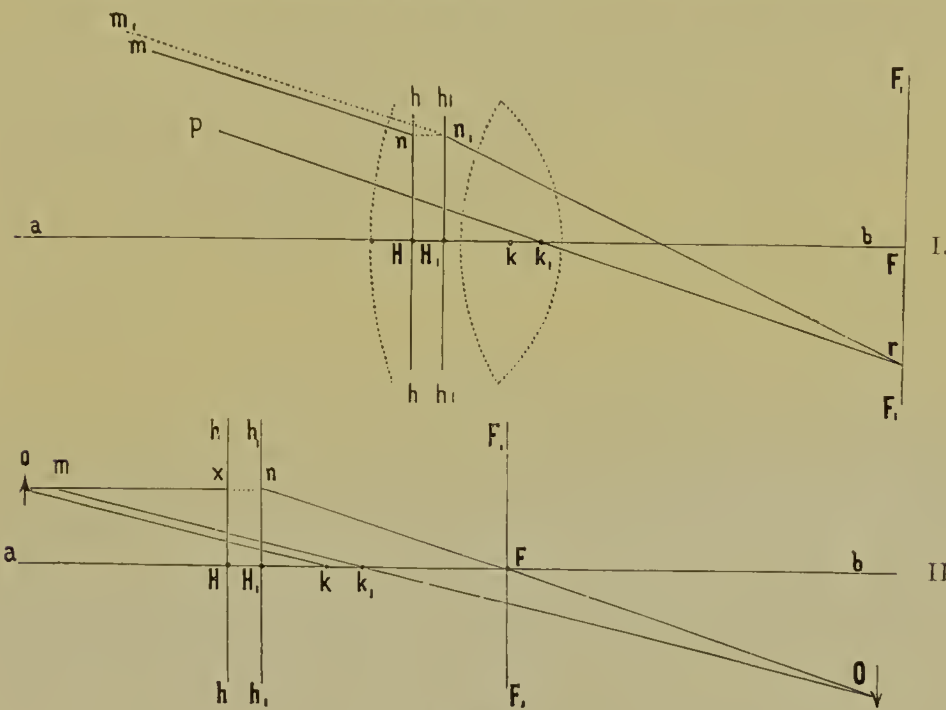


Fig. 657.

Construction of the focal point.—Let o be a luminous point (fig. 657, II.), what is the position of its image in the last medium ? Prolong from o the ray of direction $o\ k$, and make o, x parallel to $a\ b$. Both rays are prolonged in a parallel direction to the second focal plane. The ray parallel to $a\ b$ goes through F ; m, k_1 as the ray of direction passes through unrefracted. O, where n, F, and $m\ k_1$ intersect each other, is the position of the image of o.

386. DIOPTRICS—RETINAL IMAGE—OPHTHALMOMETER.—Position of the cardinal points.—The eye surrounded with air on the anterior surface of the cornea represents a concentric system of refractive media with spherical separating surfaces. In order to ascertain the course of the rays through the various media of the eye we must know the position of both principal foci of both nodal points as well as the two principal focal points. Gauss, Listing, and v. Helmholtz have calculated the position of these points. In order to make this calculation, we require to know the refractive indices of the media of the eye, the radii of the refractive surfaces, and the distance of the latter from each other. These will be referred to afterwards. (1) The **first principal point** is 2·1746 mm. ; and (2) the **second principal point** is 2·5724 mm. behind the anterior surface of the cornea. (3) The **first nodal point**, 0·7580 mm. ; and (4) the **second nodal point**, 0·3602 mm. in front of the posterior surface of the lens. (5) The **second principal focus**,

14·6470 mm. behind the posterior surface of the lens; and (6) the **first principal focus**, 12·8326 in front of the anterior surface of the cornea.

Listing's reduced eye.—The distance between the two principal points, or the two nodal points, is so small (only 0·4 mm.), that practically, without introducing any great error in the construction, we may assume *one* mean nodal or principal point lying between the two nodal or principal points. By this simple procedure we gain *one* refractive surface for all the media of the eye, and only *one* nodal point, through which all the rays of direction from without must pass without being refracted. This schematic simplified eye is called "**the reduced eye**" of Listing.

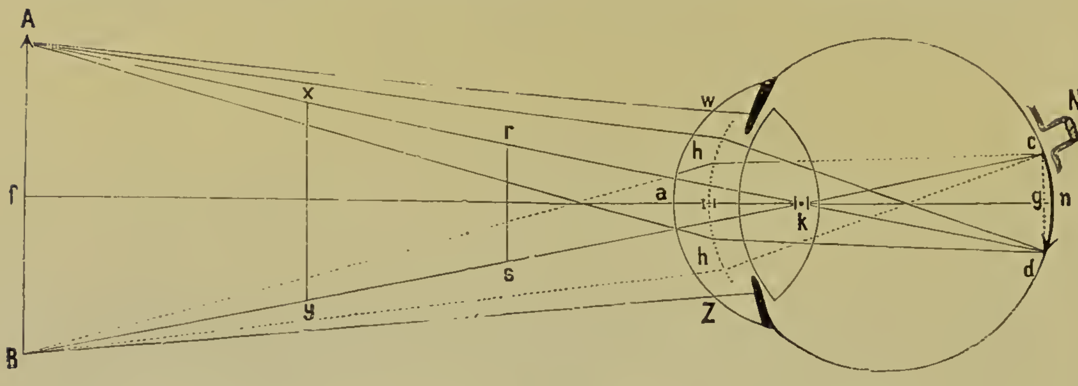


Fig. 658.

Fig. 658.—Mode of formation of an image on the retina.

Formation of the retinal image.—Thus, the construction of the image on the retina becomes very simple. In distinct vision, the **inverted image** is formed on the retina. Let A B represent an object placed vertically in front of the eye (fig. 658). A pencil of rays passes from A into the eye; the ray of direction, A *d*, passes without refraction through the nodal point, *k*. Further, as the focal point for the luminous point, A, is upon the retina, all the rays proceeding from A must reunite in *d*. The same is true of the rays proceeding from B, and, of course, for rays sent out from an intermediate point of the body, A B. The retinal image is, as it were, a mosaic, composed of innumerable foci of the object. As all the rays of direction must pass through the common **nodal point**, *k*, this is also called the "**point of intersection of the visual rays.**"

The inverted image on the retina is easily seen in the excised eye of an albino rabbit, by holding up any object in front of the cornea and observing the inverted image through the transparent coats of the eyeball.

The size of the retinal image may also be calculated, provided we know the size of the object, and its distance from the cornea. As the two triangles, A B *k* and *c d k* are similar, A B : $c\,d = f\,k$: $k\,g$, so that $c\,d = (\text{A B}, k\,g) : f\,k$. All these values are known, viz., $k\,g = 15{\cdot}16$ mm.; further, $f\,k = a\,k \times a\,f$, where $a\,f$ is measured directly, and $a\,k = 7{\cdot}44$ mm. The size of A B is measured directly.

The angle, A *k* B, is called the **visual angle**, and of course it is equal to the angle *c k d*. It is evident that the nearer objects, *x y*, and *r s*, must have the same visual angle. Hence, all the three objects, A B, *x y*, and *r s*, give a retinal image of the same size. Such objects, whose ends when united with the nodal point form a visual angle of the same size, and consequently form retinal images of the same size, have the same "**apparent size.**"

In order to determine the optical cardinal points by calculation, after the method of Gauss, we must know the following factors:—

1. **The refractive indices**: for the cornea, 1·377; aqueous humour, 1·377; lens,

1·454 (as the mean value of all the layers); vitreous humour, 1·336; air being taken as 1, and water 1·335.

2. **The radii of the spherical refractive surfaces**: of the cornea, 7·7 mm.; of the anterior surface of the lens, 10·3; of the posterior, 6·1 mm.

3. **The distance of the refractive surfaces**: from the vertex of the cornea to the anterior surface of the lens, 3·4 mm.; from the latter to the posterior surface of the lens (axis of the lens), 4 mm.; diameter of the vitreous humour, 14·6 mm. The total length of the optic axis is 22·0 mm.

[**Kühne's Artificial Eye.**—The formation of an inverted image, and the other points in the dioptrics of the eye can be studied most effectively on Kühne's artificial eye, the course of the rays of light being visible in water tinged with eosine, æsculin, or milk.]

Ophthalmometer.—This is an instrument to enable us to measure the radii of the refractive media of the eye. As the normal curvature cannot be accurately measured on the dead eye, owing to the rapid collapse of the ocular tunics, we have recourse to the process of Kohlrausch, for calculating the radii of the refrac-

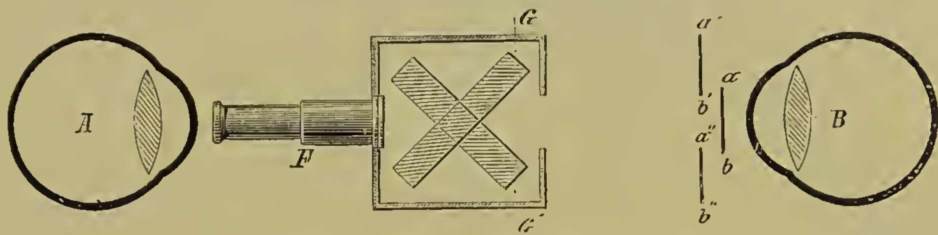


Fig. 659.
Scheme of the ophthalmometer of Helmholtz.

tive surfaces from the size of the reflected images in the living eye. The *size of a luminous body is to the size of its reflected image as the distance of both to half the radius of the convex mirror.* Hence, it is necessary to measure the size of the reflected image. This is done by means of the ophthalmometer of Helmholtz (fig. 659).

The apparatus is constructed on the following principle:—If we observe an object through a glass plate placed obliquely, the object appears to be displaced laterally; the displacement becomes greater the more obliquely the plate is moved. Suppose the observer, A, to look through the telescope, F, which has the plate, G, placed obliquely in front of the *upper* half of its objective, he sees the corneal reflected image, *a b*, of the eye, B, and the image appears to be displaced laterally, viz., to *a' b'*. If a second plate, G, be placed in front of the *lower* half of the telescope, but placed in the opposite direction, so that both plates, corresponding to the middle line of the objective, intersect at an angle, then the observer sees the reflected image, *a b*, displaced laterally to *a'' b''*. As both glass plates rotate round their point of intersection, the position of both is so selected, that both reflected images just touch each other with their inner margins, (so that *b'* abuts closely upon *a''*). The size of the reflected image can be determined from the size of the angle formed by both plates, but we must take into calculation the thickness of the glass plates and their refractive indices. The size of the corneal image, and also that in the lens, may be ascertained in the passive eye, and also in the eye accommodated for a near object, and the length of the radius of the curved surface may be calculated therefrom (*Helmholtz and others*).

Fluorescence.—All the media of the eye, even the retina, are slightly fluorescent; the lens most, the vitreous humour least (*v. Helmholtz*).

Erect Vision.—As the **retinal image is inverted**, we must explain how we see objects *upright*. By a *psychical* act, the impulses from any point of the retina are again referred to the exterior, in the direction through the nodal point; thus the stimulation of the point *d* is referred to A, that of *c* to B (fig. 658). The reference of the image to the external world happens thus, that all points appear to lie in a surface floating in front of the eye, which is called the **field of vision**. The field of vision is the inverted surface of the retina projected externally; hence, the field

of vision appears erect again, as the inverted retinal image is again projected externally but inverted (fig. 658).

That the stimulation of any point is again projceted in an inverse direction through the nodal point is proved by the simple experiment, that pressure upon the *outer* aspect of the eyeball is projected or referred to the *inner* aspect of the field of vision. The entoptical phenomena of the retina are similarly projected externally and inverted; so that, *e.g.*, the entrance of the optic nerve is referred externally to the yellow spot (sec § 393). All sensations from the retina are projected externally.

387. **ACCOMMODATION OF THE EYE.**—According to No. 2 (p. 922), the rays of light proceeding from a luminous point, *e.g.*, a flame, and acted upon by a collecting (convex) lens, are brought to a focus or focal point, which has always a definite relation to the luminous object. If a projection-surface or screen be placed at this distance from the lens, a real and inverted image of the object is obtained upon the screen. If the screen be placed nearer to the lens (fig. 651, IV., *a*, *b*), or farther away from it (*c*, *d*), no distinct image of the object is formed, but **diffusion circles** are obtained; because, in the former case, the rays have not united, and in the latter, because the rays, after uniting, have crossed each other and become divergent. If the luminous point be brought nearer to, or removed farther from, the lens, in order to obtain a distinct image, in every case, the screen must be brought nearer, or removed from the lens, to keep the same distance between the lens and the screen. If, however, the screen be fixed permanently, whilst the distance between the luminous point and the lens varies, a distinct image can only be obtained upon the screen, provided the lens, as the luminous point approaches it, becomes more convex, *i.e.*, refracts the rays of light more strongly—conversely, when the distance between the luminous point and the lens becomes greater, the lens must become less curved, *i.e.*, refract less strongly.

In the eye, the projection surface or screen is represented by the retina, which is permanently fixed at a certain distance; but the eye has the power of forming distinct images of near and distant objects upon the retina, so that the refractive power, *i.e.*, the form of the crystalline lens in the eye, must undergo a change in curvature corresponding in every case to the distance of the object.

Accommodation.—By the term "accommodation of the eye" is understood that property of the eye whereby it forms distinct images of distant as well as near objects upon the retina. [It is important to remember that we cannot see a near object and a distant one with equal distinctness *at the same time*, and hence arises the necessity for accommodation.] This power depends upon the fact that the **crystalline lens alters its curvature**, becoming more convex (thicker), or less curved (flatter), according to the distance of the object. When the lens is absent from the eyeball, accommodation is impossible (*Th. Young*, *Donders*—p. 916).

During **rest** [or **negative accommodation**], or when the eye is passive, it is accommodated for the *greatest distance*, *i.e.*, images of objects placed at an infinite distance (*e.g.*, the moon) are formed upon the retina. In this case, rays coming from such a distance are practically *parallel* and when they enter the eye are in the *passive normal* eye (**emmetropic**) brought to a focus on the retina. When looking at a distant object, a distinct image is formed on the retina without the aid of any muscular action.

That distant objects are seen without the aid of any muscular action is shown by the following considerations:—(1) With the normal, or emmetropic eye, we can see distant objects clearly and distinctly, without experiencing any feeling of effort. On opening the eyelids after a long period of rest, the objects at a distance are at once distinctly visible in the field of vision. (2) If, in consequence of paralysis of the mechanism of accommodation (*e.g.*, through paralysis of the oculomotor nerve—§ 345, 7), the eye is unable to focus images of objects placed at different distances, still distinct images are obtained of distant objects. Thus, paralysis of the mechanism of accommodation is always accompanied by inability to focus a near object, never a distant object. A temporary paralysis occurs with the same results when a solution of atropin or duboisin is dropped into the eye, and also in poisoning with these drugs (§ 392).

When the eye is accommodated for a **near object**, [**positive accommodation**], the lens is thicker, its anterior surface is more curved (**convex**), and projects farther into the anterior chamber of the eye (*Cramer*, 1851, *v. Helmholtz*, 1853). The mechanism producing this result is the following:—During **rest**, the lens is kept somewhat flattened against the vitreous humour lying behind it, by the tension of the stretched zonule of Zinn, which is attached round the margin of the lens (fig.

660, Z). When the muscle of accommodation, the ciliary muscle (*l*, *m*), contracts, it pulls forward the margin of the choroid, so that the zonule of Zinn in intimate relation with it is **relaxed**. [When we accommodate for a **near** object, the **ciliary muscle contracts**, pulls forward the choroid, relaxes the zonule of Zinn, and this in turn diminishes the tension of the anterior part of the capsule of the lens.] The lens assumes a more curved form, in virtue of its **elasticity**, so that it becomes more convex as soon as the tension of the zonule of Zinn, which keeps it flattened, is diminished (fig. 661). As the posterior surface of the lens lies in the saucer-shaped unyielding depression of the vitreous humour, the **anterior surface** of the lens in becoming more **convex** must necessarily protrude more forwards.

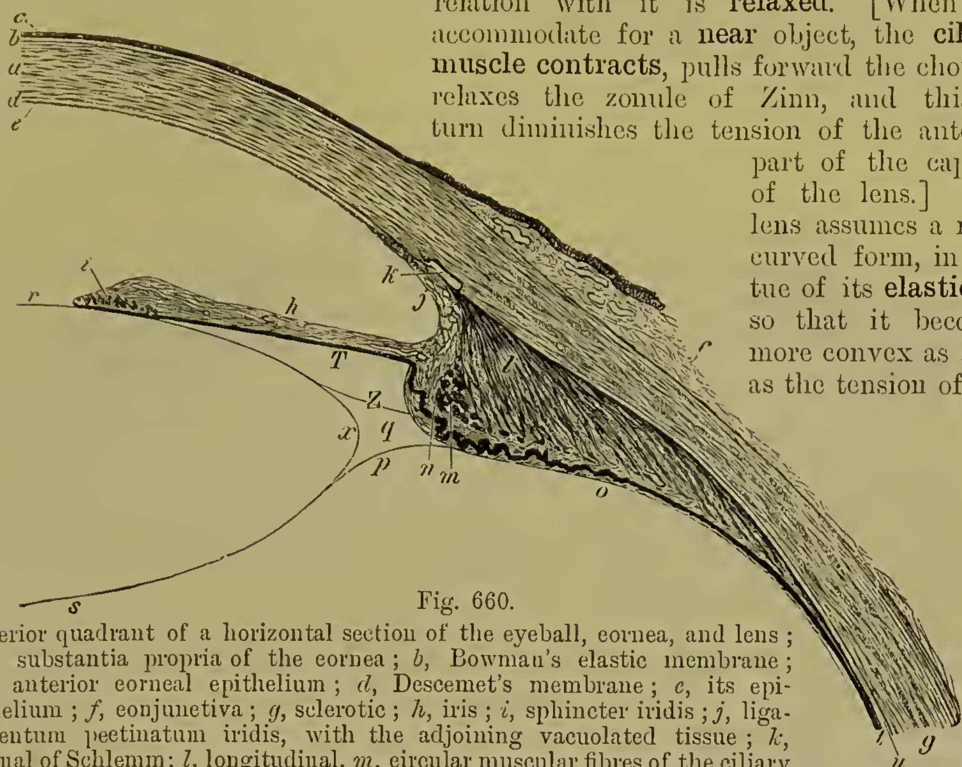


Fig. 660.
Anterior quadrant of a horizontal section of the eyeball, cornea, and lens; *a*, substantia propria of the cornea; *b*, Bowman's elastic membrane; *c*, anterior corneal epithelium; *d*, Descemet's membrane; *e*, its epithelium; *f*, conjunctiva; *g*, sclerotic; *h*, iris; *i*, sphincter iridis; *j*, ligamentum pectinatum iridis, with the adjoining vacuolated tissue; *k*, canal of Schlemm; *l*, longitudinal, *m*, circular muscular fibres of the ciliary muscle; *n*, ciliary process; *o*, cilary part of the retina; *q*, canal of Petit, with Z, zonule of Zinn in front of it; and *p*, the posterior layer of the hyaloid membrane; *r*, anterior, *s*, posterior part of the capsule of the lens; *t*, choroid; *u*, perichoroidal space; T, pigment epithelium of the iris; *x*, margin of the lens.

Nerves.—According to Hensen and Völckers, the origin of the nerves of accommodation lies in the most anterior root-bundles of the oculomotorius. Stimulation of the posterior part of the floor of the third ventricle causes accommodation; if a part lying slightly posterior to this be stimulated, contraction of the pupil occurs. On stimulating the limit between the third ventricle and the aqueduct, there results contraction of the internal rectus muscle, while stimulation of the other parts around the *iter* causes contraction of the superior rectus, levator palpebræ, rectus inferior, and inferior oblique muscles.

Proofs.—That the **lens alters its curvature** during accommodation is proved by the following facts:—

1. **Purkinje-Sanson's Images.**—If a lighted candle be held at one side of the eye, or if light be allowed to fall on the eye through two triangular holes, placed above each other and cut in a piece of cardboard, in the latter case the observer will see three pairs of reflected images [in the former, three images]. The brightest and most distinct image (or pair of images) is **erect** and is produced by the anterior surface of the **cornea** (fig. 662, *a*). The second image (or pair of images) is also **erect**. It is the largest, but it is not so bright (*b*), and it is reflected by the **anterior surface** of the **lens**. (The size of a reflected image from a convex mirror is greater the longer the radius of curvature of the reflecting surface.) The latter image

lies 8 mm. *behind* the plane of the pupil. The third image (or pair of images) is of medium size and medium brightness—it is **inverted** and lies nearly in the plane of the pupil (*c*). The posterior capsule of the lens, which reflects the last image, acts like a concave mirror. If a luminous object be placed at a distance from a con-

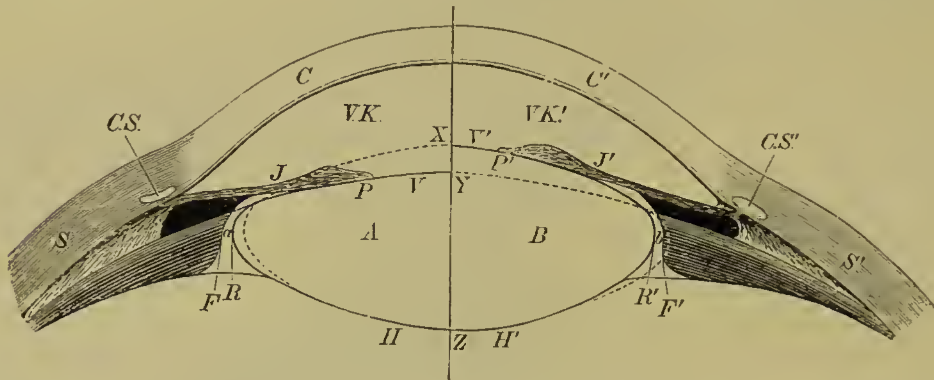


Fig. 661.

Scheme of accommodation for near and distant objects. The right side of the figure represents the condition of the lens during accommodation for a near object and the left side when the eye is at rest. The letters indicate the same parts on both sides; those on the right side are marked with a dash; *A*, left, *B*, right half of the lens; *C*, cornea; *S*, sclerotic; *C.S.*, canal of Schlemm; *V.K.*, anterior chamber; *J*, iris; *P*, margin of the pupil; *V*, anterior surface; *H*, posterior surface of the lens; *R*, margin of the lens; *F*, margin of the ciliary processes; *a* and *b*, space between the two former; the line *Z*, *X*, indicates the thickness of the lens during accommodation for a near object; *Z*, *Y*, the thickness of the lens when the eye is passive.

cave mirror, its inverted, diminished, *real* image lies close to the focus towards the side of the object. If the images be studied when the observed eye is passive, *i.e.*, in the phase of negative accommodation, on asking the person experimented upon to accommodate his eye for a near object, at once a change in the relative position and size of some of the images is apparent. The middle pair of images reflected by the anterior surface of the lens diminish in size and approach each other (*b*), which depends upon the fact that the anterior surface of the lens has become more convex. At the same time, the image (or pair of images) comes nearer to the image formed by the cornea ($a_{,}$ and $c_{,}$) as the anterior surface of the lens lies nearer to the cornea. The other images (or pairs of images) neither change their size nor position. Helmholtz, with the aid of the ophthalmometer, has measured the diminution of the radius of curvature of the anterior surface of the lens during accommodation for a near object.

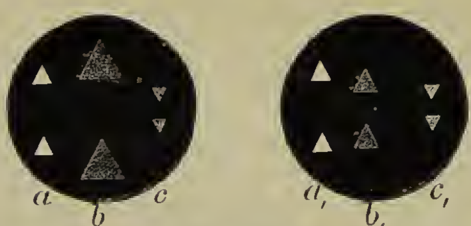


Fig. 662.

Sanson-Purkinje's images. *a*, *b*, *c*, during negative, and $a_{,,}$ $b_{,,}$ $c_{,,}$ positive accommodation.

[**Phakoscope.**—These images may be readily shown by means of the phakoscope of v. Helmholtz (fig. 663). It consists of a triangular box, with its angles cut off, and blackened inside. The observer's eye is placed at *a*, while on the opposite side of the box are two prisms, *b*, b^1; the observed eye is placed at the side of the box opposite to C. When a candle is held in front of the prisms, *b* and b^1, three pairs of images are seen in the observed eye. Ask the person to accommodate for a distant object, and note the position of the images. On pushing up the slide C with a pin attached to it, and asking him to accommodate for the pin, *i.e.*, for a near object, the position and size of the middle images chiefly will be seen to alter as described above.]

2. In consequence of the increased curvature of the lens during accommodation for a near

object, the refractive indices within the eye must undergo a change. According to v. Helmholtz the annexed measurements obtain in negative and positive accommodation respectively.

Accommodation.	Negative—Mm.	Positive—Mm.
Radius of the cornea,	8	8
Radius of anterior surface of lens,	10	6
Radius of posterior surface of lens,	6	5·5
Position of the vertex of the outer surface of the lens behind the vertex of the cornea,	3·6	3·2
Position of the posterior vertex of the lens,	7·2	7·2
Position of the anterior focal point,	12·9	11·24
Position of the first principal point,	1·94	2·03
Position of the second principal point,	6·96	6·51
Position of the posterior focal point behind the anterior vertex of the cornea,	22·23	20·25

3. **Lateral view of the pupil.**—If the passive eye be looked at from the side, we observe only a small black strip of the pupil, which becomes broader as soon as the person experimented on accommodates for a near object, as the whole pupil is pushed more forwards.

4. **Focal Line.**—If light be admitted through the cornea into the anterior chamber, the "focal line" formed by the concave surface of the cornea falls upon the iris. If the experiment be made upon a person whose eye is accommodated for a distant object, so that the line lies near the margin of the pupil, it gradually recedes towards the scleral margin of the iris, as soon as the person accommodates for a near object, because the iris becomes more oblique as its inner margin is pushed forward.

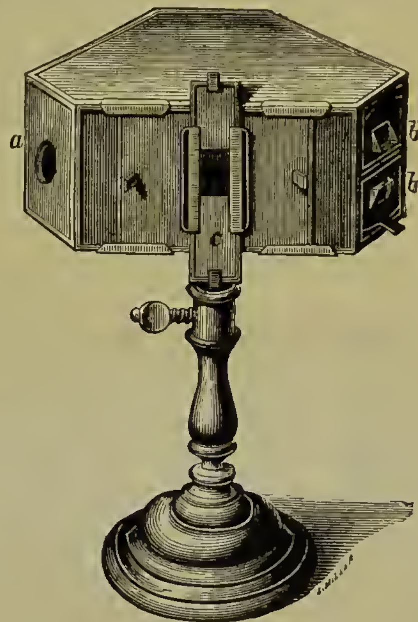


Fig. 663.

Phakoscope of Helmholtz.

5. **Change in Size of Pupil.**—On accommodating for a **near** object, the **pupil contracts**, while in accommodation for a **distant** object, it **dilates** (*Descartes*, 1637). The contraction takes place slightly after the accommodation (*Donders*). This phenomenon may be regarded as an associated movement, as both the ciliary muscle and the sphincter pupillæ are supplied by the oculomotorius (§ 345, 2, 3). A reference to fig. 660 shows that the latter also directly supports the ciliary muscle; as the inner margin of the iris passes inwards (towards *r*), its tension tends to be propagated to the ciliary margin of the choroid, which also must pass inwards. The ciliary processes are made tense, chiefly by the ciliary muscle (tensor choroideæ). Accommodation can still be performed, even though the iris be absent or cleft.

6. **Internal Rotation of the eye.**—On rotating the eyeball inwards, accommodation for a near object is performed involuntarily. As rotation of both eyeballs inwards takes place when the axes of vision are directed to a *near* object, it is evident that this must be accompanied involuntarily by an accommodation of the eye for a near object.

7. **Time for Accommodation.**—A person can accommodate from a near to a distant object (which depends upon relaxation of the ciliary muscle) much more rapidly than conversely, from a distant to a near object (*Vierordt, Aeby*). The process of accommodation requires a longer time the nearer the object is brought to the eye (*Vierordt, Völckers and Hensen*). The time necessary for the image reflected from the anterior surface of the lens to change its place during accommodation is less than that required for subjective accommodation (*Aubert and Angelucci*).

8. **Line of Accommodation.**—When the eye is placed in a certain position during accommo-

dation, we may see not *one* point alone distinctly, but a whole series of points behind each other. Czermak called the line in which these points lie the *line of accommodation*. The more the eye is accommodated for a distant object, the longer does this line become. All objects placed at a greater distance from the eye than 60 to 70 metres appear equally distinct to the eye. The line becomes shorter the more we accommodate for a near object—*i.e.*, when we accommodate as much as possible for a near object a second point can only be seen indistinctly at a *short* distance behind the object looked at.

9. The nerves concerned in the mechanism of accommodation are referred to under *Oculomotorius* (§ 345, and again in § 704).

Scheiner's Experiment.—The experiment which bears the name of Scheiner (1619) serves to illustrate the refractive action of the lens during accommodation for a near object, as well as for a distant object. Make two small pin-holes (S, *d*) in a piece of cardboard (fig. 664, K K_1), the holes being nearer to each other than the diameter of the pupil. On looking through these holes, S, *d*, at two needles (*p* and *r*) placed behind each other, then on accommodating for the *near* needle (*p*), the far needle (*r*) becomes double and inverted. On accommodating for the **near** needle (*p*), of course the rays proceeding from it fall upon the retina at the focus (p_1); while the rays coming from the far needle (*r*) have *already* united and crossed in the vitreous humour, whence they diverge more and more and form two pictures ($r_{,}$, $r_{,,}$) on the retina. If the *right* hole in the cardboard (*d*) be closed, the *left* picture on the retina ($r_{,,}$) of the double images of the far needle disappears. An analogous result is obtained on accommodating for the **far** needle (R). The near needle (P) gives a double image ($P_{,}$, $P_{,,}$), because the rays from it have not yet come to a focus. On closing the *right* hole ($d_{,}$), the *right* double image ($P_{,}$), disappears (*Porterfield*). When the eye of the observer is accommodated for the *near* needle, on closing one aperture the double image of the distant point disappears on that side; but if the eye is accommodated for the *distant* needle, on closing one hole the crossed image of the near needle disappears.

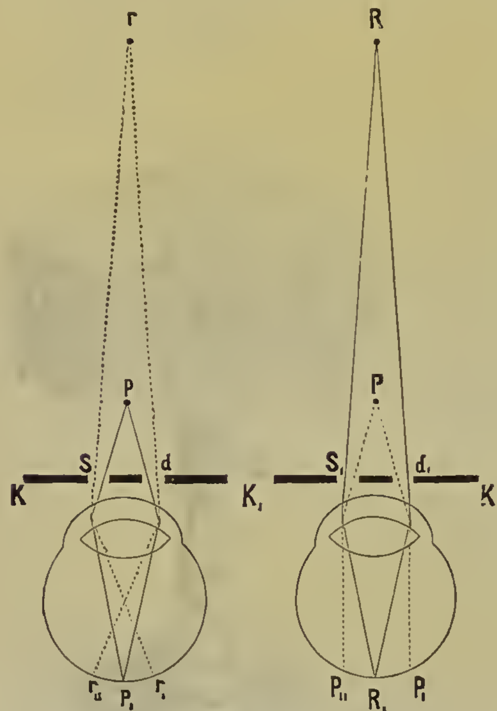


Fig. 664.
Scheiner's Experiment.

388. REFRACTIVE POWER OF THE EYE—ANOMALIES OF REFRACTION.—The limits of distinct vision vary very greatly in different eyes. We distinguish the **far point [p.r., punctum remotum]** and the **near point [p.p., punctum proximum]**; the former indicates the distance to which an object may be removed from the eye, and may still be seen distinctly; the latter, the distance to which any object may be brought to the eye, and may still be seen distinctly. The distance between these two points is called the **range of accommodation.** The types of eyeball are characterised as follows—

1. **The normal** or **emmetropic eye** is so arranged when at *rest* that parallel rays (fig. 665, *r*, *r*) coming from the most distant objects can be focussed on the retina (r_1). The *far* point, therefore, is $= \infty$ (infinity). When accommodating as much as possible for a near object, whereby the convexity of the lens is increased (fig. 665, *a*), rays from a luminous point placed at a distance of 5 inches are still

focussed on the retina, *i.e.*, the *near point* is = 5 inches (1 inch = 27 mm.). The range of accommodation, [or the "**range of distinct vision**"], therefore, is from 5 inches (10–12 cm.) to ∞.

2. **The short-sighted**, or **myopic eye** (long eye) cannot, *when at rest*, bring parallel rays from infinity to a focus on the retina (fig. 666). These rays decussate within the vitreous humour (at O), and after crossing form diffusion circles upon the retina. The object must be removed from the *passive* eye to a distance of 60 to 120 inches (to *f*), in order that the rays may be focussed on the retina. The passive myopic eye, therefore, can only focus *divergent* rays upon the retina. The *far point*, therefore, lies abnormally near. With an intense effort at accommodation, objects at a distance of 4 to 2 inches, or even less, from the eye may be seen distinctly. The *near* point, therefore, lies abnormally near; the *range of accommodation* is diminished.

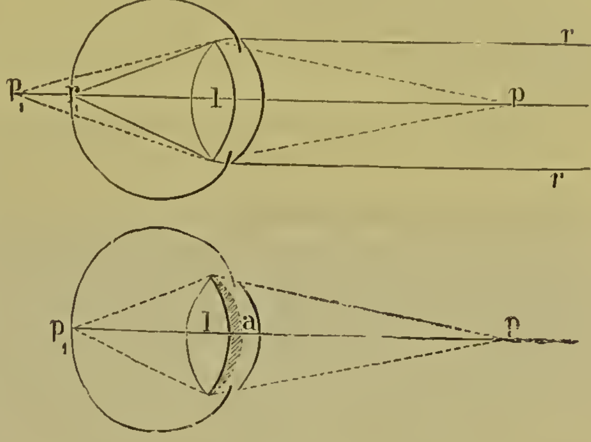


Fig. 665.
Condition of refraction in the normal *passive* eye and during *accommodation.*

Short - sightedness, or **myopia**, usually depends upon congenital, and frequently hereditary, elongation of the eyeball. This anomaly of the refractive media is easily **corrected** by using a **diverging lens** **(concave)**, which makes parallel rays divergent, so that they can then be brought to a focus on the retina. It is remarkable that most children are myopic when they are born. This myopia, however, depends upon a too-curved condition of the cornea and lens, and on the lens being too near to the cornea. As the eye grows, this short-sightedness disappears. Amongst the **causes** of myopia in children are the continued activity of the ciliary muscle in reading, writing, &c., especially in a bad light, or when the reader is in an awkward position, or the continued convergence of the eyeballs, whereby the external pressure upon the eyeball is increased.

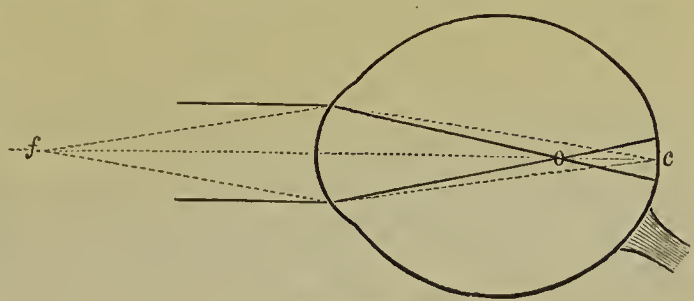


Fig. 666.
Myopic eye.

3. **The long-sighted** or **hypermetropic eye**, hyperoptic ("flat eye") when at *rest*, can only cause convergent rays to come to a focus on the retina (fig. 667). Distinct images can only be formed when the rays proceeding from objects are rendered convergent by means of a convex lens, as parallel rays would come to a focus behind the retina (at *f*). All rays proceeding from natural objects are either

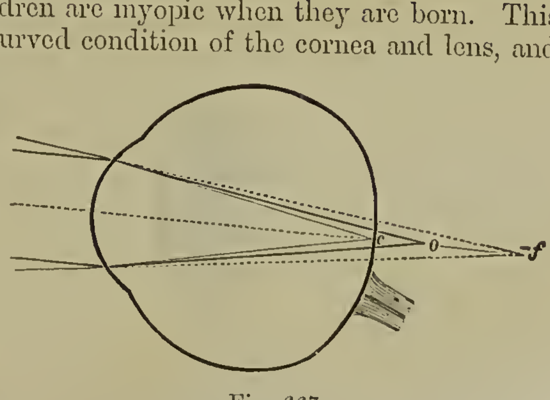


Fig. 667.
Hypermetropic eye.

divergent, or at most nearly parallel, never convergent. Hence, a long-sighted person, when the eye is *passive*, *i.e.*, is *negatively* accommodated, cannot see distinctly without a convex lens. When the ciliary muscle contracts, slightly convergent, parallel, and even slightly divergent rays may be focussed, according to the increasing degree of the accommodation. The *far point* of the eye is negative, the *near point* abnormally distant (over 8 to 80 inches), while the *range of accommodation* is infinitely great.

The **cause** of hypermetropia is abnormal shortness of the eye, which is generally due to imperfect development in all directions. It is **corrected** by using a **convex** lens.

[**Defective Accommodation.**—In the **presbyopic eye**, or **long-sighted eye** of old people, the near point is farther away than normal, but the far point is still unaffected. In such cases, the person cannot see a near object distinctly, unless it be held at a considerable distance from the eye. It is due to a defect in the mechanism of accommodation, the lens becoming somewhat flatter, less elastic, and denser with old age, while the ciliary muscle becomes weaker. In hypermetropia, on the contrary, the mechanism of accommodation may be perfect, yet from the shape of the eye the person cannot focus on his retina the rays of light from a near object. In presbyopia the range of distinct vision is diminished. The defect is remedied by weak **convex** glasses. The defect usually begins about forty-five years of age.]

Estimation of the Far Point—Snellen's Types.—In order to determine the *far point* of an eye, gradually bring nearer to the eye objects which form a visual angle of 5 minutes (*e.g.*, Snellen's small type letters, or the *medium* type, 4 to 8, of Jaeger), until they can be seen distinctly. The distance from the eye indicates the far point. In order to determine the far point of a *myopic* person, place at 20 inches distant from the eye the same objects which give a visual angle of 5 minutes, and ascertain the *concave lens* which will enable the person to see the objects distinctly. To estimate the *near point*, bring small objects (*e.g.*, the finest print) nearer and nearer to the eye, until it finally becomes indistinct. The distance at which one can still see distinctly indicates the near point.

Optometer.—The optometer may also be used to determine the **near and far points.** A small object, *e.g.*, a needle, is so arranged as to be movable along a scale, along which the eye to be investigated can look as a person looks along the sight of a rifle. The needle is moved as near as possible, and then removed as far as possible, in each case as long as it is seen distinctly. The distance of the near and far point and the range of accommodation can be read off directly upon the scale (*Gräfe*).

389. FORCE OF ACCOMMODATION.—Force.—The range of accommodation, which is easily determined experimentally, does not by itself determine the proper *power* or *force* of accommodation. The measure of the latter depends upon the *mechanical work* done by the muscle of accommodation, or the ciliary muscle. Of course this cannot be directly determined in the eye itself. Hence, this force is measured by the *optical effect*, which results in consequence of the change in the shape of the lens, brought about by the energy of the contracting muscle.

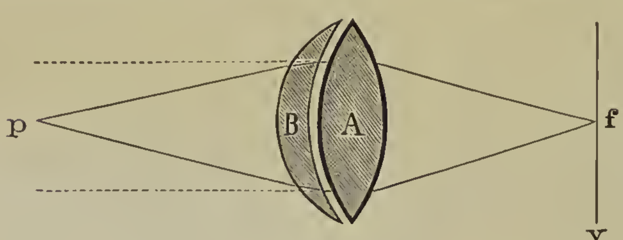


Fig. 668.

In the **normal eye**, during the passive condition, the rays coming from infinity, and therefore parallel (which are dotted in fig. 668), are focussed upon the retina at *f*. If rays coming from a distance of 5 inches (p. 930) are to be focussed, the whole available energy of the ciliary muscle must be brought into play to allow the lens to become more convex, so that the rays may be brought to a focus at *f*. The energy of accommodation, therefore, produces an *optical effect* in as far as it increases the convexity of the anterior surface of the passive lens (A), by the amount indicated by B. Practically, we may regard the matter as if a new convex lens (B) were added to the existing convex lens (A). What, therefore, must be the focal distance of the lens (B), in order that rays coming from the near point (5 inches) may be focussed upon the retina at *f*? Evidently the lens B must make the diverging rays coming from *p*, parallel, and then A can focus

them at *f*. Convex lenses cause those rays proceeding from their *focal points* to pass out at the other side as parallel rays (§ 385, 1.). Hence, in our case, the lens must have a focal distance of 5 inches. The normal eye, therefore, with the far point $= \infty$, and the near point $=$ 5 inches, has a power of accommodation equal to a lens of 5 inches focal distance. When the lens by the energy of accommodation is rendered more powerfully refractive, the increase (B) can readily be eliminated by placing before the eye a *concave lens* which possesses exactly the opposite optical effect of the increase of accommodation (B). Hence it is possible to indicate the power (force) of accommodation of the eye by a lens of a definite focal distance, *i.e.*, by the optical effect produced by the latter. Therefore, according to Donders, the measure of the force of accommodation of the eye is the reciprocal value of the focal distance of a concave lens, which, when placed before the accommodated eye, so refracts the rays of light coming from the near point (p) as if they came from the far point.

Example.—We may calculate the force of the accommodation according to the following formula:—$\frac{1}{x} = \frac{1}{p} - \frac{1}{r}$, *i.e.*, the force of accommodation, expressed as the dioptric value of a lens (of x inch focal distance), is equal to the difference of the reciprocal values of the distances of the near point (p) and of the far point (r) of the eye. In the *emmetropic* eye, as already mentioned, $p=5$, $r=\infty$. Its force of accommodation is therefore $\frac{1}{x} = \frac{1}{p} - \frac{1}{\infty}$, so that $x=5$, *i.e.*, it is equal to a lens of 5 inches focal distance. In a *myopic* eye, $p=4$, $r=12$, so that $\frac{1}{x} = \frac{1}{4} - \frac{1}{12}$, *i.e.*, $x=6$. In another myopic eye, with $p=4$ and $r=20$, then $x=5$, which is a normal force of accommodation. Hence, it is evident that two different eyes, possessing a very different *range* of accommodation, may nevertheless have the same *force* of accommodation. **Example.**—The one eye has $p=4$, $r=\infty$, the other, $p=2$, $r=4$ In both cases, $\frac{1}{x} = \frac{1}{4}$, so that the force of accommodation of both eyes is equal to the dioptric value of a lens of 4 inches focal distance. Conversely, two eyes may have the same range of accommodation, and yet their force of accommodation be very unequal. **Example.**—The one eye has $p=3$, $r=6$; the other $p=6$, $r=9$. Both, therefore, have a range of accommodation of 3 inches. For these, the force of accommodation, $\frac{1}{x} = \frac{1}{3} - \frac{1}{6}$, $x=6$; and $\frac{1}{x} = \frac{1}{6} - \frac{1}{9}$, $x=18$.

Relation of range to force of accommodation.—The *general law* is, that the *ranges* of accommodation of two eyes being equally great, then their *forces* of accommodation are equal, provided that their near points are the same. If the *ranges* of accommodation for both eyes are equally great, but their near points unequal, then the *forces* of accommodation are also unequal—the latter being greater in the eyes with the smallest near point. This is due to the fact that every difference of distance *near* a lens has a much greater effect upon the image as compared with differences in the distance *far* from a lens. The emmetropic eye can see distinctly objects at 60 to 70 metres, and even to infinity, without accommodation.

While p and r may be directly estimated in the emmetropic and myopic eyes, this is impossible with the hypermetropic (long-sighted) eye. The far point in the latter is negative; indeed, in very pronounced hypermetropia even the near point may be negative. The far point may be estimated by making the hypermetropic eye practically a normal eye by using suitable convex lenses. The *relative* near point may then be determined by means of the lens.

Even from the 15th year onwards the power of accommodation is generally diminished for near objects—perhaps this is due to a diminution of the elasticity of the lens (*Donders*).

390. SPECTACLES.—The focal distance of concave (diverging), as well as convex (converging) spectacles, depends upon the refractive index of the glass (usually 3 : 2), and on the length of the radius of curvature. If the curvature of both sides of the lens is the same (biconcave or biconvex), then with the ordinary refractive index of glass, the focal distance is the same as the radius of curvature. If one surface of the lens is plane, then the focal distance is twice as great as the radius of the spherical surface. Spectacles are arranged according to their *focal distance in inches*, but a lens of shorter focal distance than 1 inch is generally not used. They may also be arranged according to their *refractive power*. In this case, the refractive power of a lens of 1 inch focus is taken as the unit. A lens of 2 inches focus refracts light only half as much as the unit measure of 1 inch focus; a lens of 3 inches focus refracts $\frac{1}{3}$ as strongly, &c. This is the case both with convex and concave lenses, the latter, of course, having a negative focal distance; thus, "concave—$\frac{1}{8}$," indicates that a concave lens diverges the rays of light one-eighth as strongly as the concave lens of 1 inch (negative) focal distance.

Choice of Spectacles.—Having determined the *near* point in a myopic eye, of course we require to render parallel the divergent rays coming from the far point, just as if they came from infinity. This is done by selecting a concave lens of the focal distance of the far point. The greatest distance is the far point of the emmetropic eye. Suppose a myopic eye with a far point of 6 inches, then such a person requires a *concave* lens of 6 inches focus to enable him to see distinctly at the greatest distance. Thus, in a myopic eye, the distance of the far point

from the eye is directly equal to the focus of the (weakest) concave lens, which enables one to see distinctly objects at the greatest distance. These lenses generally have the same number as the spectacles required to correct the defect. **Example.**—A myopic eye with a far point of 8 inches requires a *concave* lens of 8 inches focus, *i.e.*, the concave spectacles No. 8. For the **hypermetropic** (long-sighted) eye, the focal distance of the strongest **convex** lens, which enables the hypermetropic eye to see the most distant objects distinctly, is at the same time the distance of the far point from the eye **Example.**—A hypermetropic eye which can see the most distant objects with the aid of a *convex* lens of 12 inches focus has a far point of 12; the proper spectacles are convex No. 12.

[**Diopter** or **Dioptric.**—The focal length of a lens used to be expressed in inches; and as the unit was taken as 1 inch, necessarily all weaker lenses were expressed in fractions of an inch. In the method advocated by Donders, the standard is a lens of a focal distance of 1 metre (39·370 English inches, about 40 inches), and this unit is called a *dioptric.* Thus, the standard is a weak lens, so that the stronger lenses are multiples of this. Hence, a lens of 2 dioptrics = one of about 20 inches focus; 10 dioptrics = 4 inches focus; and so on. The lenses are numbered from No. 1, *i.e.*, 1 dioptric onwards. It is convenient to use signs instead of the words convex and concave. For convex the sign *plus* + is used, and for concave the sign *minus* –. Thus a + 4·0 means a convex lens of 4 dioptrics, and a – 4·0 = a concave lens of 4 dioptrics.]

In all cases of myopia or hypermetropia, the person ought to wear the proper spectacles. In a **myopic eye**, when the far point is still more than 5 inches, the patient ought always to wear spectacles; but generally the working distance, *e.g.*, for reading, writing, and for handicrafts, is about 12 inches from the eye. If the person desires to do finer work (etching, drawing), requiring the object to be brought nearer to the eye, so as to obtain a larger image upon the retina, then he should either remove the spectacles altogether or use a weaker pair.

The **hypermetropic person** ought to wear his convex spectacles when looking at a near object, and especially when the illumination is feeble, because then, owing to the dilatation of the pupil, the diffusion circles of the eye tend to become very pronounced. It is advisable to wear at first convex spectacles which are slightly too strong. **Cylindrical lenses** are referred to under *Astigmatism.* Spectacles provided with dull-coloured or blue glasses are used to protect the retina when the light is too intense. **Stenopaic spectacles** are narrow diaphragms placed in the front of the eye, which cause it to move in a definite direction in order to see through the opening of the diaphragm.

391. CHROMATIC AND SPHERICAL ABERRATION, ASTIGMATISM. —**Chromatic Aberration.**—All the rays of *white* light, which undergo refraction, are at the same time broken up by dispersion into a bundle of rays which, when they are received on a screen, form a spectrum. This is due to the fact that the different colours of the spectrum possess different degrees of refrangibility. The violet rays are refracted most strongly; the red rays least.

A white point on a black ground does not form a sharp simple image on the retina, but many coloured points appear after each other. If the eye is accommodated so strongly as to focus the violet rays to a sharp image, then all the other colours must form concentric diffusion circles, which become larger towards the red. In the centre of all the circles, where all the colours of the spectrum are superposed, a white point is produced by their mixture, while around it are placed the coloured circles. The distance of the focus of the red rays from that of the violet in the eye = 0·58 to 0·62 mm. The focal distance for red is, according to v. Helmholtz, for the reduced eye, 30·524 mm.; for violet, 20·140 mm. Thus, the near and far points for violet light are nearer each other than in the case of red light; white objects, therefore, appear reddish when beyond the far point, but when nearer than the near point they are violet. Hence, the eye must accommodate more strongly for red rays than for violet, so that we judge red objects to be nearer us than violet objects placed at an equal distance (*Brücke*).

Monochromatic, or Spherical Aberration.—Apart from the decomposition or dispersion of white light into its components—the rays of white light, proceeding from a point if transmitted through refractive spherical surfaces—we find that, before the rays are again brought to a focus, the *marginal* rays are more strongly refracted than those passing through the central parts of the lens. Hence, there is not *one* focus but many. In the eye this defect is naturally **corrected** by the *iris*, which, acting as a diaphragm, cuts off the marginal rays (fig. 658), especially when the lens is most convex, when the pupil also is most contracted. In addition, the margin of the lens has less refractive power than the central substance; lastly, the margins of the refractive

spherical surfaces of the eye are less curved towards their margins than the parts lying nearer to the optical axis. Compare the form of the cornea (p. 906) and the lens (p. 916).

Imperfect Centring of the Refractive Surfaces.—The sharp projection of an image is somewhat interfered with by the fact that the refractive surfaces are not exactly centred (*Brücke*). Thus, the vertex of the cornea is not exactly in the termination of the optic axis; the vertices of both surfaces of the lens, and even the different layers of the lens itself, are not exactly in the optic axis. The variations, however, and the disturbances produced thereby, are very small indeed.

Regular Astigmatism.—When the curvature of the refractive surfaces of the eye is unequally great in its different meridians, of course the rays of light cannot be united or focussed in one point. Generally, in such cases, the cornea is more curved in its vertical meridian and least in the horizontal (as is shown by ophthalmometric measurements, p. 925). The rays passing through the vertical meridian come to a focus, *first*, in a horizontal focal line; while the rays entering horizontally unite afterwards in a vertical line. There is thus no common focus for the light-rays in the eye; hence the name "**astigmatism.**" The lens also is unequally

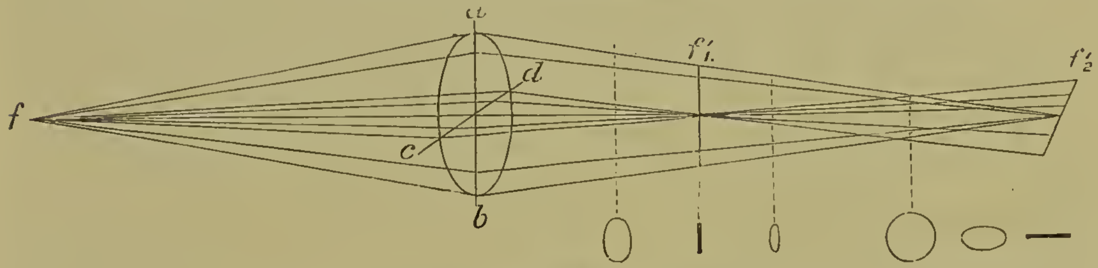


Fig. 669.
Action of an astigmatic surface on a cone of light (*Frost*).

curved in its meridians, but it is the reverse of the cornea; consequently, a part of the inequality of the curvature of the cornea is thereby compensated, and only a part of it affects the rays of light. The emmetropic eye has a *very slight* degree of this inequality (normal astigmatism). If two very fine lines of equal thickness be drawn on white paper, so as to intersect each other at right angles, it will be found that, in order to see the horizontal line quite sharply, the paper must be brought slightly nearer to the eye, than when we focus the vertical line. When the inequality of curvature of the meridians is considerable, of course exact vision is no longer possible.

Fig. 669 shows the effect of an astigmatic surface on the rays of light. Let *a b c d* be such a surface, and suppose diverging rays to proceed from *f*. The rays passing through *c d* come to a focus at f_1, while those passing through the vertical meridian are focussed at f_2. The outline of the cone of rays between *a b c d* and f_2 varies, as shown in the figure. At a certain part it is oval, with its axis vertical, at another the long axis of the oval is horizontal, while at other places it is circular, or the rays are focussed in a horizontal or vertical line.]

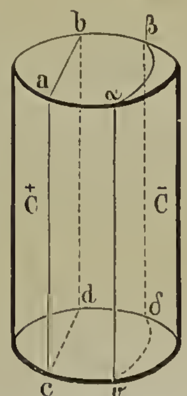


Fig. 670.
Cylindrical glasses for astigmatism.

Correction of Astigmatism.—This condition is corrected by a **cylindrical lens**, *i.e.*, a lens so cut as to be without curvature in one direction, while in the other direction (vertical to the former) it is curved. The lens is placed in front of the eye, so that the direction of its curvature coincides with the direction of least curvature of the eye (*v. Helmholtz, Knapp, Donders*). The section C *a b c d* of the cylindrical lens (fig. 670) represents a plano-convex, the section C $\alpha\ \beta\ \gamma\ \delta$, a concavo-convex lens.

[**Test.**—Draw two lines of equal thickness at right angles to each other. An astigmatic person cannot see both lines with equal distinctness at the same time, one line will appear thicker than the other. Or a series of lines radiating from a centre may be used (**astigmatic clock**, fig. 671) when that line which is parallel to the astigmatic meridian will be seen most distinctly; while, with the vertical meridian most curved, it would be the vertical line.]

Irregular Astigmatism.—Owing to the radiate arrangement of the fibres in the interior of the

crystalline lens, and in consequence of the unequal course of the fibres within the different parts of one and *the same meridian* of the lens, the rays of light passing through one meridian of the lens, cannot all be brought to one focus. Hence, we do not obtain a distinct sharp image of distant luminous points, such as stars or street lamps, but we see a radiate jagged figure provided with rays. The same obtains on holding a piece of cardboard with a small hole in it towards the light, at a distance from the eye slightly greater than the far point. Slight degrees of this irregular astigmatism are normal, but when it is highly developed it greatly interferes with vision, by forming *several* foci of an object instead of one (**Polyopia monocularis**). Of course this condition cannot obtain in an eye devoid of a lens.

392. **Iris.—Functions.**—1. The iris acts like a **diaphragm** in an optical apparatus by cutting off the marginal rays, which, if they entered the eye, would cause *spherical aberration*, and thus produce indistinct vision (fig. 658).

2. As the pupil contracts strongly in a bright light, and dilates when the light is feeble, it **regulates** the amount of **light** entering the eye; thus, fewer rays enter the eye when the light is strong than when it is feeble.

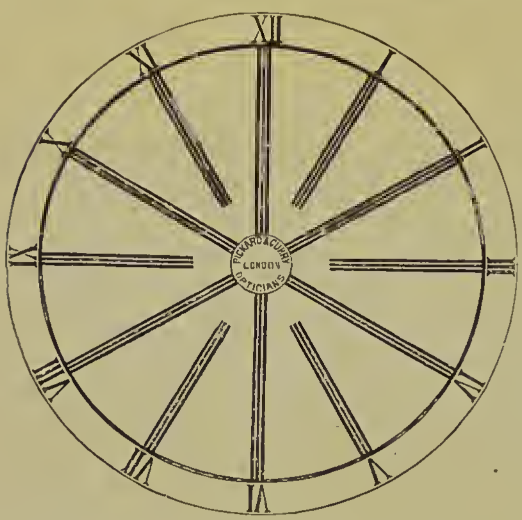


Fig. 671.
Astigmatic clock for testing astigmatism.

3. To a certain extent it supports the action of the ciliary muscle.

Muscles and Nerves.—The iris is usually described as being provided with **two** *sets of muscular fibres*—the **sphincter**, which immediately surrounds the pupil and is supplied by the oculomotorius (§ 345, 2), and the **dilator pupillæ** (p. 910), supplied chiefly by the cervical sympathetic (§ 356, A, 1), and the trigeminus (§ 347, 3). Both muscles stand in an *antagonistic* relation to each other (§ 345), the pupil dilates moderately after section or paralysis of the oculomotorius, owing to the contraction of the dilator fibres which are supplied by the cervical sympathetic; conversely the pupil contracts when the sympathetic is divided or extirpated (*Petit*, 1727). When both nerves are stimulated simultaneously, the pupil contracts, so that the excitability of the oculomotorius overcomes the sympathetic.

[The **existence of a dilator pupillæ muscle** is not universally recognised, and in fact some observers doubt its existence. The muscular nature of the radial fibres in the posterior limiting membrane of the iris is denied by Grünhagen, while Koganei regards these as in no case muscular, and the dilating fibres as represented by fibres radiating from the iris. These fibres are well developed in birds and the otter, exist in traces in the rabbit, and are absent in man. Gaskell points out that in this case the size of the pupil must in part depend on the elasticity of the radial fibres of the iris, while the dilator nerve-fibres must act on the sphincter fibres, causing them to relax. Gaskell groups the sphincter of the iris with those muscles "supplied by two nerves of opposite character, the one motor, the other inhibitory." The dilatation of the pupil caused by stimulation of the cervical sympathetic is usually explained by the hypothesis that this nerve contains motor fibres, which act on the dilator fibres. Grünhagen thought that it might be due chiefly to the constriction of the blood-vessels of the iris; Gaskell suggests that the nerve acts on the sphincter muscle, and is the inhibitory nerve of that muscle, dilatation taking place because the sphincter is normally in a condition of tonic contraction, and also because the posterior limiting membrane is elastic.]

Nerves of the Iris.—Arnstein and A. Meyer have studied the mode of termination of the nerve-fibres in the iris. All the medullated nerve-fibres lose their white sheaths after a time; most of the fibres (*motor*) in the region of the sphincter consist of naked bundles of fibrils. A network of very delicate *sensory* nerves lies under the anterior epithelium. Numerous fibrils pass to the capillaries and arteries as *vaso-motor nerves*. [Many ganglionic cells are intercalated in the course of the fibres.]

Movements of the iris occur under the following conditions:—

1. **Action of light on the retina** causes (according to its intensity and amount) a corresponding **contraction of the pupil**; the same effect is produced by *stimulation of the optic nerve itself* (*Herbert Mayo*). This movement is a reflex act, [the *afferent* nerve being the optic and the *efferent* the oculomotorius; the impulse is transferred from the former to the latter in a centre situated somewhere below the corpora quadrigemina (fig. 672, C)].

The older observers locate the centre in the corpora quadrigemina, the recent observers in the medulla oblongata (§ 362). *Both* pupils always react, although only one retina be stimulated; generally under normal circumstances both contract to the same extent (*Donders*), owing to the intercentral communication [coupling] of the two pupillo-constricting centres. [This is called consensual contraction of the pupil.] After section of the optic nerve the pupil dilates, and subsequent section of the oculomotorius no longer produces any further dilatation (*Knoll*).

2. **The centre for the dilator fibres of the pupil** (pupillo-dilating centre) is excited by *dyspnœic blood* (§ 367, 8). If the dyspnœa ultimately passes into asphyxia, the dilatation of the pupil diminishes. Of course, if the peripheral dilating fibres (§ 247, 3) [*e.g.*, the sympathetic nerve in the neck] be previously divided, this effect cannot take place, as the dyspnœic blood acts on the *centre* and not on the nerve-fibres.

3. The **centre**, as well as the subordinate "**cilio-spinal region**" of the spinal cord (§ 362, 1), is also capable of being excited **reflexly**; painful stimulation of sensory nerves, in addition to causing protrusion of the eyeballs (§ 347), a fact proved in the case of persons subjected to torture, produces dilatation of the pupils (*Arndt, Bernard, Westphal, Luchsinger*); while a similar effect is caused by labour pains, a loud call in the ear, stimulation of the nerves of the sexual organs, and even by slight tactile impressions (*Foà and Schiff*). According to Bechterew, the foregoing results are due to inhibition of the light-reflex in the sense expressed in § 361, 3.

4. The **condition of the blood-vessels** of the iris influences the size of the pupil; all conditions causing injection or congestion of these vessels contract the pupil, all conditions diminishing them dilate it. The pupil, therefore, is **contracted** by *forced expiration*, which prevents the return of venous blood from the head; momentarily by every *pulse-beat*, owing to the diastolic filling of the arteries; *diminution of the intraocular pressure*, *e.g.*, after puncture of the anterior chamber, because, owing to the diminished intraocular pressure, there is less resistance to the passage of blood into the blood-vessels of the iris (*Hensen and Völckers*); paralysis of the vaso-motor fibres of the iris (§ 347, 2). Conversely, the pupil is **dilated** by conditions the reverse of those already mentioned, and also by *strong muscular exertion*, whereby blood flows freely into the dilated muscular blood-vessels; also, when death takes place. The condition of the filling of the blood-vessels also explains the fact that the pupil dilated with atropin becomes smaller when a part of the sympathetic in the upper cervical ganglion, carrying the vaso-motor fibres of the iris, is excised; also, that after extirpation of this ganglion, atropin always causes a less diminution of the pupil on this side. The fact that when the pupil is already dilated by stimulation of the sympathetic, it is further dilated by atropin, is due to a diminished injection of the blood-vessels of the iris. If an animal with its pupils dilated with atropin be rapidly bled, the pupils contract, owing to the anæmic stimulation of the origin of the oculomotorius (*Moriggia*). The dilatation of the pupils observed in cases of neuralgia of the trigeminus is partly due to the stimulation of the dilating fibres, partly to the stimulation of the vaso-motor fibres of the iris (§ 347, 2).

5. **Contraction of the pupil** occurs as an **associated movement**, during *accommodation* for a near object (p. 929, 5), and when the *eyeballs are rotated inwards*, which is the case during *sleep* (p. 847).

Conversely, intense movements of the iris, caused by variations in the brightness of dazzling illumination, *e.g.*, of the electric light, are followed by disturbing associated movements of the ciliary muscle (*Ljubinsky*). In certain movements discharged from the medulla oblongata (forced respiration, chewing, swallowing, vomiting), dilatation of the pupil occurs as a kind of *associated movement*.

[**Argyll Robertson Pupil.**—In this condition the pupil does not contract to light, although it contracts when the eye is accommodated for a near object, vision usually being normal.]

[The lesion is situated in those structures connecting the afferent and efferent fibres at their central ends (at Δ in fig. 672), *i.e.*, the connection between the corpora quadrigemina and the oculomotorius. It is most frequently found in locomotor ataxia, although it also occurs in progressive paralysis of the insane.]

Direct stimulation at the margin of the cornea causes dilatation of the pupil (*E. H. Weber*); in fact, direct stimulation of circumscribed areas of the margin of the iris causes partial contraction of the dilator fibres (*Bernstein and Dogiel*). Stimulation near the centre of the

cornea contracts the pupil (*E. H. Weber*). In addition, we must assume that the iris itself contains elements that influence the diameter of the pupil (*Sig. Mayer and Pribram*).

Our knowledge of the **action of drugs** on the iris is still very obscure. Those substances which **dilate** the pupil are called **mydriatics**, *e.g.*, **atropin**, homatropin, duboisin, daturin, and hyoscyamin.

They act chiefly by paralysing the oculomotorius. But, in addition, there must be also an effect upon the dilating fibres, for after complete paralysis (section) of the oculomotorius, the *moderate* dilatation of the pupil thereby produced (§ 345, 5) is still further increased by atropin. *Minimal doses* of atropin contract the pupil, owing to stimulation of the pupillo-constrictor fibres ; *enormous* doses cause moderate dilatation of the pupil in consequence of paralysis of the dilating as well as of the constricting nerve-fibres. Atropin acts after destruction of the ciliary [ophthalmic] ganglion (*Hensen and Völckers*) [and division of all the nerves except the optic], and in the excised eye (*De Ruyter*), [so that atropin is a **local mydriatic.** In moderate doses it paralyses the nervous terminations of the 3rd nerve (but not in birds whose iris contains striped muscle), and in larger doses it also paralyses the muscular fibres]. [**Cocaine**, or cucaine, is obtained from the leaves of Erythroxylon coca. When applied locally it acts as a powerful local anæsthetic, and hence it is very useful for operations about the muco-cutaneous orifices. A 4 per cent. solution dropped into the eye produces complete insensibility of the cornea in a few minutes. It causes dilatation of the pupils, though they react to light and to the movements of accommodation. It also causes temporary paralysis of accommodation, a sensation of heaviness and coldness of the eyeball, enlargement of the palpebral fissure, constriction of the small peripheral vessels, and slight lachrymation.]

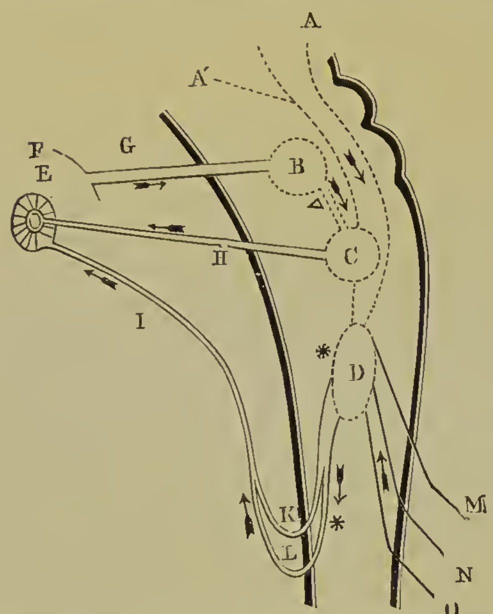


Fig. 672.

Scheme of the nerves of the iris. B, centrum optici ; C, oculomotor centre ; D, dilator centre (spinal) ; E, iris ; G, optic nerve ; H, oculomotor (sphincter) roots ; I, sympathetic (dilator) ; K, L, anterior roots ; M, N, O, posterior roots ; Δ, seat of lesion, causing pupillary immobility ; * probable seat of lesion, causing myosis.

Myotics are those substances which **contract** the pupil :—**Physostigmin** (= Eserin, the alkaloid of Calabar bean), nicotin, pilocarpin, muscarin, morphia, according to some observers (*Grünhagen*) cause stimulation of the oculomotorius while others say they paralyse the sympathetic.

As these substances cause spasm of the ciliary muscle, it is supposed that the first of these has an analogous action on the sphincter. It is *probable* that they paralyse the dilator fibres and stimulate the oculomotor fibres. [Amongst **local myotics**, *i.e.*, those which act on the eye, some act on the muscular fibres of the iris, *e.g.*, physostigmin or eserin, while others act on the peripheral terminations of the 3rd nerve, *e.g.*, pilocarpin, muscarin. Muscarin causes very great contraction of the pupil from spasm of the circular fibres, due to its action on the 3rd nerve ; eserin, on the other hand, although contracting the pupil, also affects the dilator fibres. The contraction of the pupil due to opium is central in its cause.]

If the one pupil be contracted or dilated by these substances the other pupil conversely is dilated or contracted, owing to the change in the amount of light admitted into the eye into which the poison has been introduced. The **anæsthetics** (ether, chloroform, alcohol, &c.), when they begin to cause stupor, contract the pupil, and when their action is intense they dilate it (*Dogiel*). Chloroform, during the stage when it causes excitement (preceding the narcosis), stimulates the centre for the dilatation of the pupil ; after a time this centre is paralysed, so that the pupil no longer dilates on the application of external stimuli. Thereafter the pupillo-constrictor centre is stimulated, whereby the pupil may be contracted to the size of a pin's head ; ultimately this centre is paralysed, and the pupil becomes dilated.

Intraocular Pressure.—The movements of the iris are always accompanied by variations of the intraocular pressure. The muscles of the iris affect the intraocular pressure, in that the dilatation of the pupil increases it, while contraction of the pupil diminishes it. The increased

or diminished tension can be felt when two fingers are pressed on the eyeball. Stimulation of the sympathetic increases, while its section diminishes the pressure. **Action of Drugs.**—Atropin dropped into the eye, after producing a short temporary diminution of the tension, increases it; eserin, after a primary increase, causes a diminution of the pressure (*Graser and Hölzle*). According to Hocker, atropin diminishes the intraocular pressure, eserin first increases it and then diminishes it.

Time for Movements of Iris.—The reflex dilatation of the pupil occurs slightly later than the reflex contraction, the time in the two cases being 0·5 and 0·3 second respectively, after stimulation by light (*v. Vintschgau*). A certain *time* always elapses, until the iris, corresponding to the strength of the stimulus of light exciting the retina, "adapts" itself to produce a suitable size of the pupil (*Aubert*). Contraction of the pupil occurs very rapidly after stimulation of the oculomotorius in birds; in rabbits 0·89 second elapses after stimulation of the sympathetic, until the dilatation begins (*Arlt*).

Action of Light on Excised Eye.—Light causes contraction of the pupil in the *excised* eye of amphibians and fishes (*Arnold*). Even the iris of the eel, when cut out and placed in normal saline solution, contracts to light (*Arnold*), the green and blue rays being most active. *Increase of the temperature* causes mydriasis in the excised eye of the frog or eel, while cooling causes myosis (*H. Müller*).

[**Size of the Pupil.**—A **pupilometer** consists of a metal plate perforated with a series of holes of different sizes (fig. 673). The plate is placed just below the patient's eye, and the hole is selected which corresponds with the size of the pupil.]

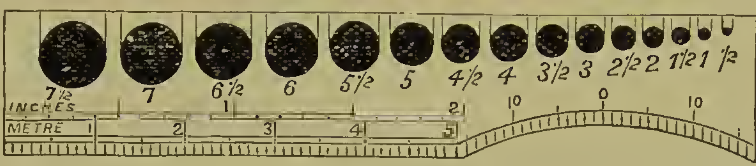


Fig. 673.
Pupilometer of Edgar Browne.

[**Gorham's Pupil Photometer.** — This ingenious instrument may be used as a **pupilometer,** and also as a **photometer.** It consists of a piece of bronzed tubing 1·9 in. long and 1·5 in. diameter (figs. 674 and 675). One end is closed by a disc or cap, which is pierced in its radii by a series of holes at distances varying from ·05 in. to ·28 in. There is a slot in the cap, which allows one pair of holes to be visible at a time, while on the cylinder is engraved the linear distance of each pair of holes. In using the instrument as a **pupilometer,** look through the open end of the tube (the bottom in fig. 675), with both eyes open, towards a sheet of white paper or the sky, when two discs of light will be seen. Then revolve the lid or cap slowly until

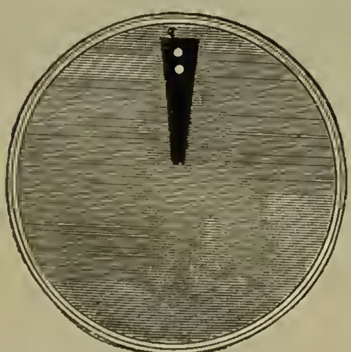


Fig. 674.

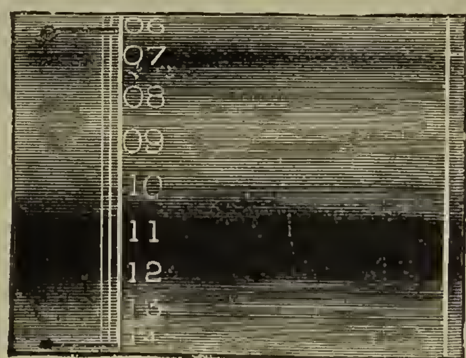


Fig. 675.

Gorham's pupil photometer. Fig. 674 shows the disc with a slot and two holes. Fig. 675 gives a side view with the diameter of the pupil marked on it. The upper end is closed by the disc, while the lower end is open.

the two white discs *just touch one another at their edges.* The decimal fraction opposite the two apertures seen on the scale outside indicates the diameter of the pupil in 100ths of an inch. When using it as a *photometer*, it is assumed that the size of the pupil gives an index of the intensity of the amount of light which influences the diameter of the pupil.]

[The following table from Beaunis shows the chief conditions which affect the pupil :—

Contraction of the Pupil.	Dilatation of the Pupil.
Stimulation of the optic nerve.	Section of the optic nerve.
Stimulation of the third cranial nerve.	Paralysis of the third cranial nerve.
Section of the fifth cranial nerve.	Stimulation of the fifth cranial nerve.
Section or paralysis of the cervical sympathetic.	Stimulation of the sympathetic.
Paralysis of the vaso-motor fibres of the iris.	Stimulation of the vaso-motor fibres of the iris.
Filling of the vessels of the iris.	Contraction of the vessels of the iris.
Light acting on the retina, or directly on the iris.	Stimulation of sensory nerves.
Accommodation for a near object.	Vision of distant objects.
Rotation of the eyeball inwards.	Rotation of the eyeball outwards.
Diminution of intra-ocular pressure.	Increase of the intra-ocular pressure.
Puncture of the anterior chamber.	Stimulation of the margin of the iris or cornea.
Expiration.	Inspiration, dyspnœa, asphyxia.
Sleep.	Syncope and approach of death.
Myotics (Calabar bean, nicotin, opium).	Mydriatics (atropin).
Anæsthetics (at first).	Anæsthetics (at the end).
Heat.	Cold.
	Strong muscular contraction.]

393. ENTOPTICAL PHENOMENA.—Entoptical phenomena depend upon the perception of objects present within the eyeball itself.

1. **Shadows** are formed upon the retina by different opaque bodies. In order to see them in one's own eye, proceed thus :—By means of a strong convex lens project a small image of a flame upon a paper screen, prick a small opening through the image of the flame, and place one eye at the other side of the screen, so that the illuminated puncture lies in the anterior focus of the

Fig. 676.

Entoptical shadows.

eye, *i.e.*, about 13 mm. in front of the cornea. As the rays proceeding from this point pass parallel through the media of the eye, a diffuse bright field of vision, surrounded by the black margins of the iris, is obtained. All dark bodies which lie in the course of the rays of light throw a shadow upon the retina, and appear as specks. There are various kinds of these shadows (fig. 676) :—

(a) The **spectrum mucro-lacrimale**, especially upon the margin of the eyelids, depending upon particles of mucus, fat globules from the Meibomian glands, dust mixed with tears, causing cloudy or drop-like retinal shadows, which are removed by winking.

(b) **Folds in the cornea.**—If the cornea be pressed laterally with the finger, wrinkled shadows, due to temporary wrinkles in the cornea, are produced.

(c) **Lens shadows.**—Bead-like or dark specks, bright and star-like figures, the former due to deposits on and in the lens, the latter to the radiate structure of the lens.

(d) **Muscæ volitantes** (*Dechales*, 1690), like strings of beads, circles, groups of balls or pale stripes, depend upon opaque particles (cells, disintegrating cells, granular fibres) in the **vitreous humour.** They move about when the eye is moved rapidly. Listing [1845] showed that one may determine pretty accurately the position of these objects. Whilst making the observation upon one's own eyes, raise or depress the source of light ; those shadows which are caused by bodies on a level with the pupil retain their relative positions in the bright fields of vision. Shadows which appear to move in the same direction as the source of light are caused by bodies which

lie in *front* of the plane of the pupil—those, however, which appear to move in the opposite direction depend upon objects behind the plane of the pupil.

2. **Purkinje's figure** (1819) depends upon the **blood-vessels within the retina**, which cast a shadow upon the most external layer of the retina, viz., upon the rods and cones, these being the parts acted upon by light. In ordinary vision we do not observe these shadows. According to v. Helmholtz, this is due to the fact that the sensibility of the shaded parts of the retina is greater, and their excitability is less exhausted than all the other parts of the retina. As soon, however, as we change the position of the shadow of the blood-vessels, instead of being directly behind, so that the blood-vessels come to lie more *laterally* and behind them, *i.e.*, upon places which do not receive shadows from the blood-vessels when the rays of light pass through the eye in the ordinary way, then the figure of the blood-vessels becomes apparent at once. All that is necessary is to cause the light to enter the eyeball obliquely. **Methods.**—(1) This may be done by passing an intense light through the sclerotic, *e.g.*, by throwing upon the sclerotic a small, bright, luminous image from a source of light. On moving the source of light, the figure of the blood-vessels moves in the same direction. (2) Look directly upwards to the sky, wink with the upper eyelid drooping, so that for a moment, corresponding to the act of winking, rays of light enter obliquely the lowest part of the pupils. (3) Look through a small aperture towards a bright sky, and move the aperture rapidly to and fro, so that from both sides of the blood-vessels shadows fall rapidly upon the nearest series of rods and cones. (4) In a darkened room look straight ahead, and move a light to and fro close under the eyes. Occasionally, whilst performing this experiment, one may see the macula lutea as a non-vascular shaded depression, and owing to the inversion of the objects, it lies on the *inner* side of the entrance of the optic nerve.

3. **Movements of the blood-corpuscles in the retinal capillaries.**—On looking, without accommodating the eye, towards a large bright surface, or through a dark blue glass towards the sun, we see bright spots, like points, forming longer or shorter chains, moving in tortuous paths. The phenomenon is, perhaps, caused by the red blood-corpuscles (in the capillaries posterior to the external granular layer) acting as small light-collecting concave discs, concentrating the light falling upon them from bright surfaces, and throwing it upon the rods of the retina. Each corpuscle must be in a special position; should it rotate, the phenomenon disappears. Vierordt, who projected the movement upon a screen, calculated, from the velocity of their motion, the velocity of the blood-stream in the retinal capillaries as equal to 0·5 to 0·75 mm. in a second, which corresponds very closely with the results obtained directly in other capillaries by E. H. Weber and Volkmann (§ 90, 4). When the carotids are compressed, the movement is slower on freeing them from the compression; during short forced expirations the movement is accelerated (*Landois*).

4. The **entoptical pulse** (§ 79, 2) depends upon the pulsating arteries irritating mechanically the rods lying outside them.

5. **Pressure Phosphenes.**—Pressure applied to the eye causes a series of phenomena:—(*a*) Pressure upon part of the eyeball causes the so-called illuminated "pressure-picture" or **phosphene**, which was known to Aristotle. As the impression upon the retina is referred to something outside the eye, the phosphene is always perceived on the side of the field of vision *opposite* to where the pressure affects the retina, *e.g.*, pressure upon the *outer* surface of the eyeball causes the flash of light to appear on the *inner* side. If the retina is not well lighted, the phosphene appears luminous; if the retina is well lighted, it appears as a dark speck, within which the visual perception is momentarily abolished. (*b*) If a uniform pressure be applied to the eyeball continuously from before backwards, as Purkinje pointed out, after some time there appear in the field of vision very sparkling variable figures which perform a wonderful fantastic play, and often resemble the sparkling effects obtained in a kaleidoscope (*v. Helmholtz*), and are probably comparable to the feeling of formication produced by pressure upon sensory nerves ("sleeping of the limbs"). (*c*) By applying equable and continued pressure, Steinbach and Purkinje observed a network with moving contents of a bluish-silvery colour, which seemed to correspond to the retinal veins. Vierordt and Laiblin observed the branching of the blood-vessels of the *choroid* as a red network upon a black ground. (*d*) According to Houdin, we may detect the position of the yellow spot by pressure upon the eyeball.

6. The **entrance of the optic nerve** may be detected on moving the eyes rapidly backwards, and especially inwards, as a fiery ring or semicircle about the size of a pea. Probably, owing to the movement of the retina, the entrance of the optic nerve is stimulated mechanically by the rapid bending. Purkinje and others observed that the ring remained persistent on turning the eye strongly inwards. If the retina be brightly illuminated, the ring appears dark, and when the field of vision is coloured, the ring has a different tint. If Purkinje's figure be produced at the same time, one may observe that the vascular trunk proceeds from this ring—a proof that the ring corresponds to the entrance of the optic nerve (*Landois*).

7. **Accommodation Spot.**—On accommodating the eye strongly towards a white surface, there appears in the middle a small bright trembling shimmer, and in its centre a coarse brown speck, about the size of a pea, is seen (*Purkinje*). If pressure be applied externally to the eyeball, this speck becomes more distinct. After having once observed the phenomenon,

occasionally on pressing laterally upon the opened eye we may see it as a bright speck in the field of vision—another proof that the intraocular pressure is increased during accommodation.

8. **Mechanical Optical Stimulation.**—On dividing the optic nerve in man, as in extirpation of the eyeball, a flash of light is observed at the moment of section by the person operated on. The section of the nerve-fibres themselves is painless, but section of the sheaths is painful.

9. The **accommodation phosphene** is the occurrence of a fiery ring at the periphery of the field of vision, seen on suddenly bringing the eyes to rest after accommodating for a long time in the dark *(Purkinje)*. The sudden tension of the zonule of Zinn resulting from the relaxation causes a mechanical stretching of the outermost part of the margin of the retina, or it may be of a part of the retina behind this. Purkinje observed the phenomenon after suddenly relaxing the pressure on the eye.

10. **Electrical Phenomenon.**—Electrical currents, when applied to the eye, cause a strong flash of light over the whole field of vision. One pole of the battery may be placed on the under eyelid and the other on the neck. The flash at closing [making] the current is strongest with an ascending current, that with opening [breaking] the current with a descending current. If a uniform continuous *ascending* current be transmitted through the closed eyes, the dark disc of the elevation at the entrance of the optic nerve appears in a whitish-*violet* field of vision; with a *descending* current, the field of vision is *reddish* and dark, in which the position of the optic nerve appears light blue (*v. Helmholtz*). If external colours are looked at simultaneously, these colours blend to form a violet or yellow with the colours looked at (*Schelske*). During the passage of the ascending current we see external objects indistinctly and *smaller* when the eyes are open; while with the descending current they are *larger* and more distinct (*Ritter*). Sometimes the position of the macula lutea appears dark on a bright ground, or the reverse, according to the direction of the current. If the current be opened [broken] the phenomena are reversed (§ 335), and the eye soon returns to rest.

11. The **yellow spot** appears sometimes as a dark circle when there is a uniform blue illumination. In a strong light the position of the yellow spot is surrounded by a bright area, twice or thrice as large, called "**Löwe's ring.**" [**Clerk-Maxwell's Experiment.**—On looking through a solution of chrome-alum in a bottle or vessel with parallel glass sides, we observe an oval rosy-purplish spot in the greenish colour of the alum. This is due to the pigment of the yellow spot.]

Haidinger's Brushes.—On directing the eye towards a source of polarised light, "Haidinger's polarised brushes" appear at the point of fixation. They are seen on looking through a Nicol's prism at a bright cloud (*v. Helmholtz*). They are bright and bluish on a surface, bounded by two neighbouring hyperbola on a white field; the dark bundle separating them is smallest in the centre and yellow. Of the various colours of homogeneous light, blue alone shows the brushes (*Stokes*). According to v. Helmholtz, the seat of the phenomenon is the yellow spot, and is due to the yellow-coloured elements of the yellow spot being slightly doubly refractive while at one part they absorb more, at another less, of the rays entering the eye.

12. Lastly, there are the visual sensations depending on **internal causes**, *e.g.*, increased bounding of the blood through the retina, as during violent coughing, increased intraocular pressure. Stimulation of the *visual areas* (§ 378, IV.) may produce spectra, which Cardanus (1550), Goethe, Nicolai, and Johannes Müller could produce voluntarily.

394. ILLUMINATION OF THE EYE.—OPHTHALMOSCOPE.—The light which enters the eye is partly absorbed by the black uveal pigment, and partly again reflected from the eye, and always in the same direction in which the rays entered the eye. By placing oneself in front of the eye of another person, of course the head, being an opaque body, cuts off a large number of rays. Owing to the position of the head, no rays of light can enter the eye; and of course none can be reflected back to the eye of the observer. Hence, the eye of the person being examined always appears black, because those rays which alone could be reflected in the direction of the eye of the observer are cut off. As soon, however, as we succeed in causing rays of light to enter the eye at the same time and in the *same* direction in which we observe the eye of another person, the fundus of the eye appears brightly illuminated.

The following simple arrangement is sufficient for the purpose (fig. 677):—Let B be the eye of the patient, A that of the observer, and let a flame be placed at x. The rays of light proceeding from x impinge upon the obliquely placed *plate of glass* (S,S), and are reflected in the direction of the dotted lines into the eye (B). The fundus of the eye appears in this position to be brightly illuminated in diffusion circles around b. As the observer (A) can see through the obliquely placed glass plate (S, S), and in the same direction as the reflected rays (x, y), he sees the retina around b brightly illuminated.

In order that this method be made available for practical purposes, we must, of course, be

able to distinguish the details, such as the blood-vessels of the fundus of the eye, the macula lutea, the entrance of the optic nerve, abnormalities of the retina, and the choroidal pigment, &c. The following considerations show us how to proceed in order to accomplish this. As already mentioned, and as fig. 658 shows, a small inverted image is formed on the retina (c, d) when we look at an object (A, B); conversely, according to the same dioptric

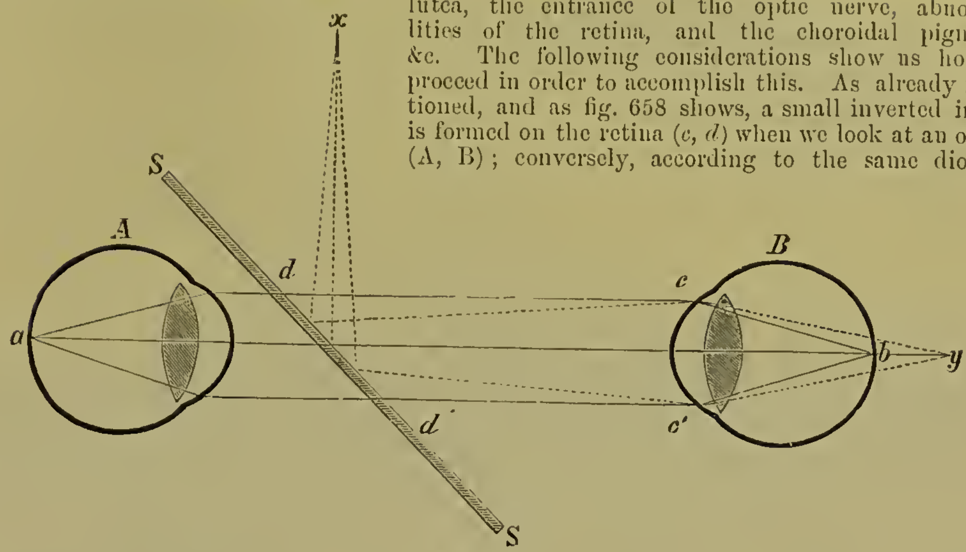


Fig. 677.

Arrangement for examining the eye of B. A, eye of observer; x, source of light; S, S, plate of glass directed obliquely, reflecting light into B.

law, an enlarged inverted real image of a small distinct area of the retina (c, d—depending on the distance for which the eye was accommodated) must be formed outside the eye (A, B). If the fundus of this eye be sufficiently illuminated, this aerial image will be correspondingly bright.

In order to see the individual parts of the retinal picture more distinctly, the observer must accommodate his own eye for the position of this image. In such circumstances the eye of the

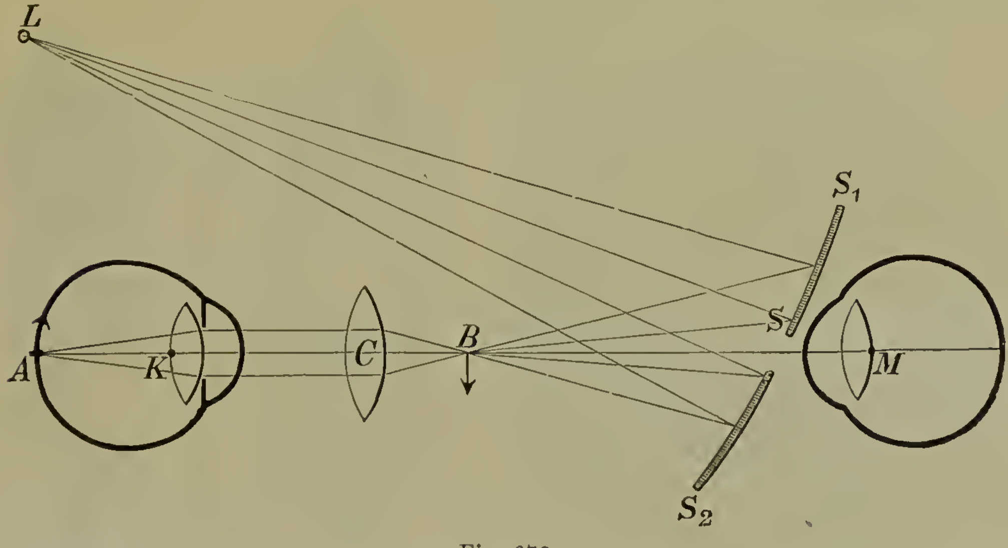


Fig. 678.

observer would be too near the observed eye. His eye when so accommodated is removed from the eye of the patient by his own visual distance, and by the visual distance of the patient. As this distance is considerable, the individual small details of the fundus cannot be seen distinctly. Further, owing to the contraction of the pupil of the patient, only a small area of the fundus can be seen, and this only under a small visual angle, quite apart from the fact that it is often impossible to accommodate for the real image of the fundus of the patient.

Hence, the eye of the observer must be brought nearer to the eye of the patient. This may be done in two ways:—(1) Either by placing in front of the eye of the patient a strong *convex lens* (of 1 to 3 inches focus—fig. 678, C). This causes the retinal image to be nearer to the eye

(at B), owing to the strong lens refracting the rays of light. The observer (M) can come nearer to the eye, and can still accommodate for the image of the fundus of the eye. (2) Or a *concave lens* is placed immediately in front of the eye of the patient (fig. 679, *o*). The rays of light

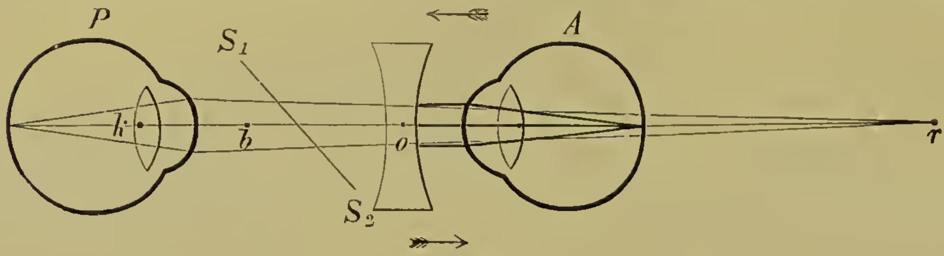


Fig. 679.

emerging from the eye of the patient (P) are either made parallel by the concave lens (*o*), and are brought to a focus on the retina of the emmetropic observer (A); or, if the lens causes the

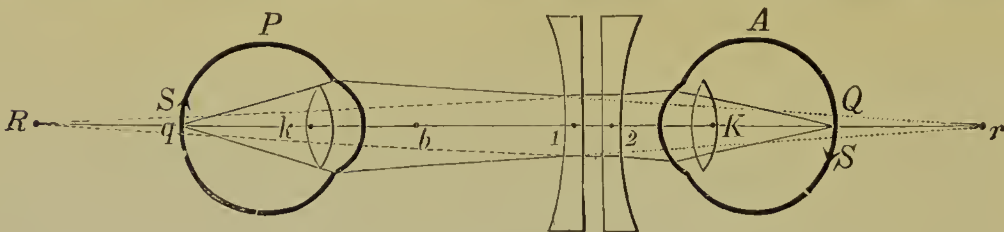


Fig. 680.

rays to diverge (fig. 680), an erect, virtual image is formed at a distance behind the eye of the patient (at R). In these cases also the observer can go much nearer to the eye of the patient.

The **ophthalmoscope** invented by v. Helmholtz enables us to examine the whole of the fundus of the eye.

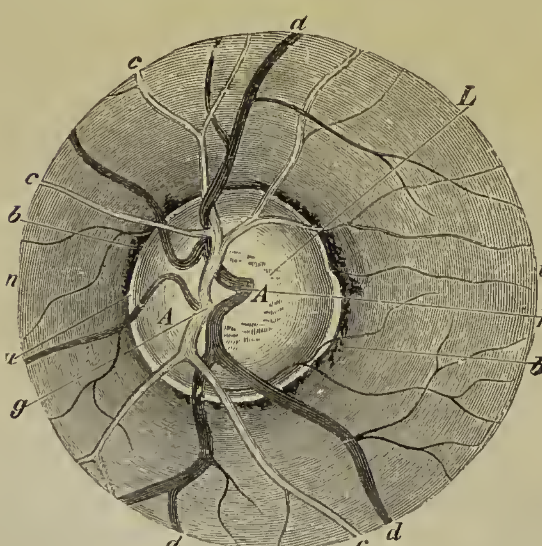


Fig. 681.

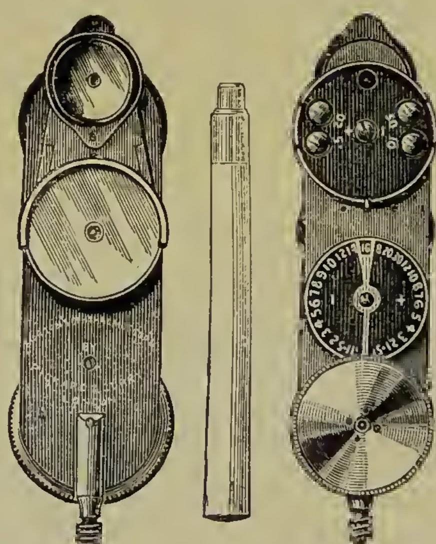


Fig. 682.

Fig. 681.—The entrance of the optic nerve with the adjacent parts of the fundus of the normal eye. *a*, ring of connective-tissue; *b*, choroidal ring; *c* arteries; *d*, veins; *g*, division of the central artery; *h*, division of the central vein; L, lamina cribrosa; *t*, temporal (outer) side; *n*, nasal (inner) side. Fig. 682.—Morton's ophthalmoscope.

[**Direct Method.**—Use a concave mirror of 20 centimetres focal distance, with a central opening. Reflect a beam of light into the patient's eye, where the rays

cross in the vitreous and illuminate the fundus of the eye. These rays again pass out of the eye and reach the observer's eye through the central hole in the mirror. If the observer be emmetropic they come to a focus on his retina. In this way all the parts of the retina are seen in their normal position, but enlarged. Hence, it is sometimes called the examination of the **upright image.** The eye of the patient and observer must be at rest, *i.e.*, be negatively accommodated, while the mirror must be brought as near as possible to the eye of the patient.]

[**Indirect Method,** by which a more general view of the fundus is obtained. Throw the light into the patient's eye by an ophthalmoscopic mirror as above, but held at a distance of about 25 cm. (10 inches) from the patient's eye. Hold a biconvex lens of 14 dioptrics focal length vertically between the mirror and the patient's eye (fig. 678), the observer looking through the hole of the mirror. What he does see is an **inverted aerial image** at B. Only a small part of the fundus oculi can be seen at one time.]

[The ophthalmoscope, besides being used for examining the interior of the eyeball, is of the utmost use in determining the existence and amount of **anomalies of refraction** in the refrac-

Fig. 683.
Frost's artificial eye.

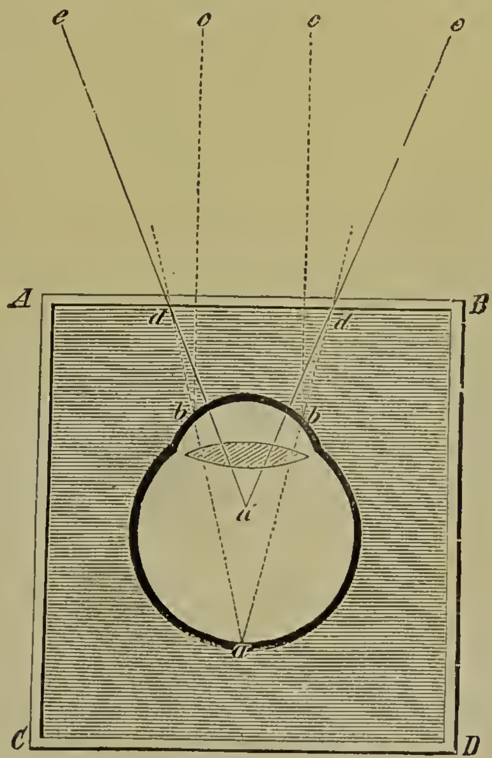


Fig. 684.
Action of the orthoscope.

tive media. For this purpose an ophthalmoscope requires to be provided with *plus* and *minus* lenses, which can be readily brought before the eye of the observer. This is readily done by an ingenious mechanism devised by Couper, and made use of in the handy students' ophthalmoscope of Morton (fig. 682). The lenses are moved by a driving-wheel on the left figure, while at the same time is indicated at a certain aperture the lens presented at the sight hole. The instrument is also provided with a movable arrangement carrying a concave mirror at either end. One of these mirrors is 10 inches in focus, and is used for indirect examination and retinoscopy, while the other is of 3 inches focus for direct examination, and is fixed at an angle of 25°.]

[Retinoscopy.—The ophthalmoscope is used also for this purpose. A beam of light is reflected into the eye by the ophthalmoscopic mirror, and the play of light and shade on the fundus oculi observed. A study of this is important in determining anomalies of refraction. For the method, the student is referred to a text-book on "Diseases of the eye."]

[**Artificial Eye.**—The student may practise the use of the ophthalmoscope on an artificial eye, such as that of Frost (fig. 683) or Perin or Priestley Smith.]

Illumination of the retina.—In order to illuminate the interior of the eye, v. Helmholtz used several plates of glass, placed behind each other, in the position of S, S, in fig. 677. Afterwards he used a plane or concave mirror of 7 inches focus (fig. 677), with a hole in the centre. Fig. 681 shows the appearance of the fundus of the eye, as seen with the ophthalmoscope. In albinos the fundus of the eye appears red, because light passes into the eye through the sclerotic and uvea, which are devoid of pigment. If a diaphragm be placed over the eye, so that the pupil alone is free, the eye appears black (*Donders*).

Tapetum.—In many animals the eyes have a bright green lustre. These eyes have a special layer, the tapetum, or the membrana versicolor of Fielding; in carnivora it consists of cells [devoid of melanin granules], in herbivora of fibres, placed between the capillaries of the choroid and the stroma of the uvea. These structures exhibit interference-colours and reflect much light, so that the coloured lustre appears in the eye (p. 914).

Oblique illumination is used with advantage for investigating the anterior chamber. A bright beam of light, condensed by a convex lens, is thrown *laterally* upon the cornea into the eye, and so directed upon the point to be investigated as to illuminate it. A point so illuminated, *e.g.*, a part of the iris, may be examined from a distance by means of a lens, or even by a microscope (*Liebreich*).

Orthoscope.—Czermak constructed this instrument, in which the eye is placed under water (fig. 684). It consists of a small glass trough with one of its walls removed. The margins of the open side are pressed firmly against the region of the eye. The eye and its surroundings form, as it were, the sixth side of the trough, which is filled with water, so that the cornea is bathed therewith. As the refractive index of water is almost the same as the refractive index of the media of the eye, the rays of light pass into the eye in a straight direction without being refracted. Hence, objects in the anterior chamber can be seen directly, as if they were not within the eye at all. Another advantage is that the objects can be brought nearer to the eye of the observer. The rays of light emerging from the point (a) of the fundus, if the eye were surrounded by air, would leave the eye as the parallel lines, b, c, b, e. Under water, these rays, a, b, continue in the direction a, b, as far as b, d, where they emerge from the water, and are bent from the perpendicular to d, e, d, e. The eye of the observer, looking in the direction e, d, sees the point, a, *nearer*, viz., in the direction e, d, a', lying at a.

395. ACTIVITY OF THE RETINA IN VISION.—I. Blind Spot.

—The **rods and cones** alone are the parts of the retina **sensitive to light**; they alone are excited by the vibrations of the ether. This is confirmed by Mariotte's experiment (1688), which proves that the entrance of the optic nerve, where rods and cones are absent, is devoid of visual sensibility. Hence it is spoken of as the "**blind spot.**"

[**Mariotte's Experiment.**—Make a cross and a circle, about 3 inches apart, upon paper (fig. 685). Look at the cross with the right eye, keeping the left eye

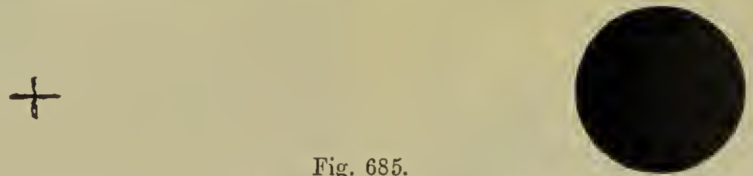


Fig. 685.
Mariotte's experiment.

closed, and hold the paper about a foot from the eye, when both the cross and the circle will be seen. Gradually approximate the paper to the eye, keeping the open eye steadily fixed on the cross; at a certain moment the circle will disappear, and on bringing the paper nearer to the eye it will reappear. The moment when the circle disappears is when its image falls upon the entrance of the optic nerve.]

Position and Size.—The entrance of the optic nerve lies about 3·5 mm. internal to the visual axis of the eyeball, in the retina. Its diameter is 1·8 mm. The apparent diameter of the blind spot in the field of vision is in a horizontal direction 6° 56′—this lies 12° 35′ to 18° 55′ horizontally from the fixed point. Eleven full moons placed side by side would disappear on the surface, and so would a human face at a distance of over 2 metres.

Proofs.—The following facts prove that the entrance of the optic nerve is insensible to light:—(1) Donders projected, by means of a mirror, the small image of a flame upon the

entrance of the optic nerve of another person, and the person had no sensation of light. But a sensation of light was experienced when the image of the flame was projected upon the neighbouring parts of the retina. (2) On combining with Mariotte's experiment the experiment which causes entoptical phenomena at the entrance of the optic nerve, this coincides with the blind spot (§ 393, 6 and 7).

Form of Blind Spot.—In order to determine the *form and apparent size of the blind spot* in one's own eye, fix the head at about 25 centimetres from a surface of white paper; select a small point on the latter and keep the eye directed towards it; then, starting from the position of the blind spot, move a white feather in all directions over the paper; whenever the tip of the feather becomes visible, make a mark at this spot. The blind spot may be mapped out in this way. It has an irregular, elliptical form from which processes proceed, due to the equally non-sensitive origins of the large blood-vessels of the retina (*Hueck*). (Mariotte concluded from his experiment that the choroid, which is perforated by the optic nerve, is the membrane sensitive to light, as the nerves are nowhere absent from the retina.)

The blind spot causes no appreciable gap in the field of vision.—As the area is not excited by light, a black spot cannot appear in the field of vision, for the sensation of black implies the presence of retinal elements, which, however, are absent from the blind spot. The circumstance, however, that in spite of the existence of an inexcitable spot during vision, no part of the field of vision appears to be *unoccupied*, is due to a psychical action. The unoccupied area of the field of vision, corresponding to the blind spot, is filled in according to probability, by a psychical process (*E. H. Weber*). Hence, when a white point disappears from a black surface, the whole surface appears to us black; a white surface, from which a black point falls on the blind spot, appears quite white; a page of print, grey throughout, &c. According to the probabilities, certain parts are supplied—parts of a circle, the middle parts of a long line, the central part of a cross. Such images, however, as cannot be constructed according to the probabilities, are not perfected, *e.g.*, the end of a line or a human face. In other cases the condition known as "*contraction*" of the field of vision tends to fill up the gap. This will be evident on looking at the nine adjoining letters, so that *e* disappears; we no longer see the three letters on each side of it in straight lines, but *b*, *f*, *h*, *d* are turned in towards *e*. The adjoining parts of the field of vision seem to extend over and around the blind spot, and thus help to compensate for the blind spot.

a	b	c
d	(e)	f
g	h	i

II. Optic Fibres inexcitable to Light.—The layer of the *fibres of the optic nerve* in the retina is *not sensitive to light.* This is proved by the fact that, in the fovea centralis, which is the area of most acute vision, there are no nerve-fibres. Further, Purkinje's figure proves that, as the arteries of the retina lie behind the optic fibres, the latter cannot be concerned in the perception of the former.

III. Rods and Cones.—The outer segments of the rods and cones have rounded outlines, and are packed close together; but natural spaces must exist between them, corresponding to the spaces that must exist between groups of bodies with a circular outline. These parts are insensible to light, so that a retinal image is composed like a mosaic of round stones. The diameter of a cone in the yellow spot is 2 to 2·5 μ (*M. Schultze*). If two images of two small points, placed very near each other, fall upon the retina, they will still be distinguished as distinct images, provided that both images fall upon two different cones. The two images on the retina need only be 3–4–5·4 μ apart, in order that each may be seen separately, for then the images fall upon *two* adjoining cones. If the distance be diminished so very much that both images fall upon *one* cone, or one upon one cone and the other upon the intermediate or cement substance, then only *one* image is perceived. The images must be further apart in the peripheral portion of the retina in order that they may be separately distinguished.

As the rounded end-surfaces of the cones do not lie exactly under each other, but are so arranged that one series of circles is adapted to the interstices of the following series, this explains why fine dark lines lying near each other appear to have alternating twists upon them, as the images of these must fall upon the cones, at one time to the right, at another to the left.

IV. The **fovea centralis** is the region of **most acute vision**, where only cones are present, and where they are very numerous and closely packed (fig. 648). The

cones are less numerous in the peripheral areas of the retina, and consequently vision is much less acute in these regions. We may therefore conclude that the cones are more important for vision than the rods. When we wish to see an object distinctly we involuntarily turn our eyes so that the retinal image falls upon the fovea centralis. In doing this, we are said to "*fix*" our eyes upon an object. The line drawn from the fovea to the object is called the **axis of vision** (fig. 686, *S r*). It forms an angle of only 3·5–7° with the "*optical axis*" (*O A*), which unites the

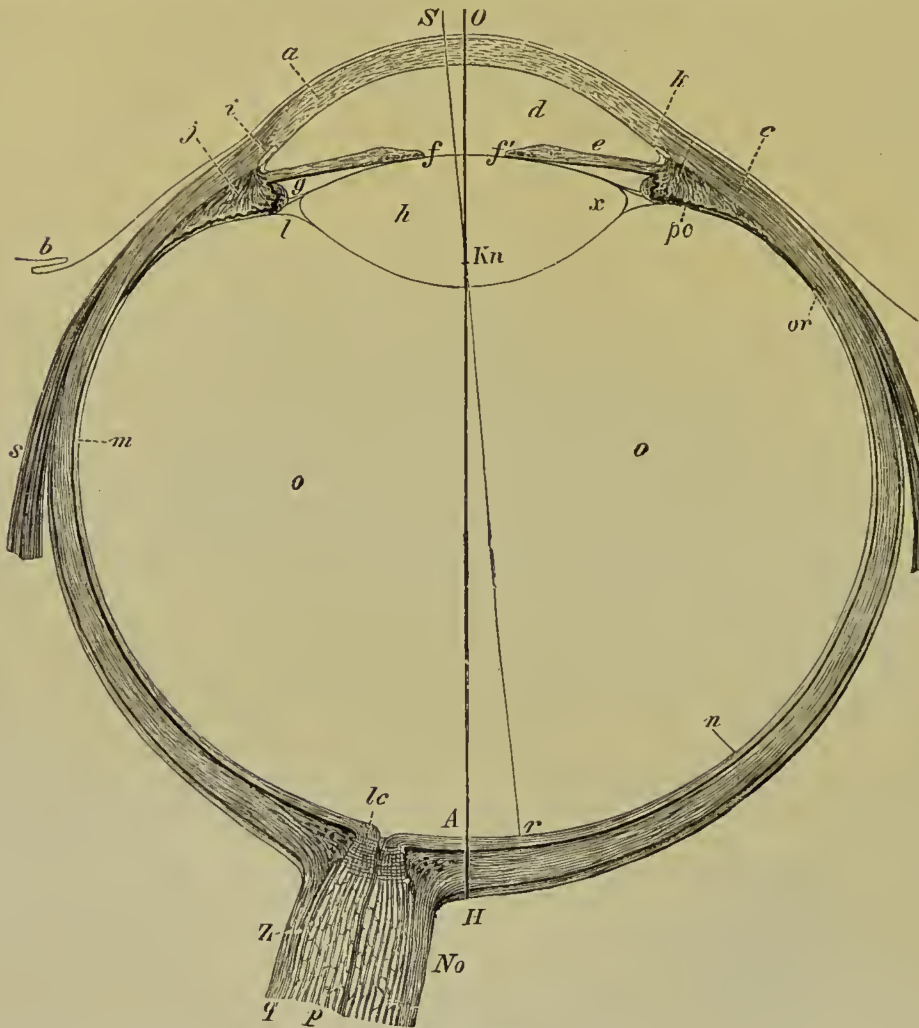


Fig. 686.

Horizontal section of the right eye. *a*, cornea; *b*, conjunctiva; *c*, sclerotic; *d*, anterior chamber containing the aqueous humour; *e*, iris; *f f'*, pupil; *g*, posterior chamber; *l*, Petit's canal; *j*, ciliary muscle; *k*, corneo-scleral limit; *i*, canal of Schlemm; *m*, choroid; *n*, retina; *o*, vitreous humour; *No*, optic nerve; *q*, nerve-sheaths; *p*, nerve-fibres; *lc*, lamina cribrosa. The line *O A* indicates the optic axis; *S r*, the axis of vision; *r*, the position of the fovea centralis.

centres of the spherical surfaces of the **refractive media** of the eye. The point of intersection, of course, lies in the nodal point (*Kn*) of the lens (p. 948). The term "**direct vision**" is applied to vision when the direction of the axis of vision is in line with the object [*i.e.*, when the image of the object falls directly on the fovea centralis].

"**Indirect vision**" occurs when the rays of light from an object fall upon the **peripheral parts** of the retina. Indirect vision is much less acute than the

direct. Still the periphery of the retina is in a high degree capable of distinguishing movements, changes, or intermission of visual impressions (*Exner*).

To test the acuity of direct vision, draw two fine parallel lines close to each other, and gradually remove them more and more from the eye, until both appear *almost* to unite and form one line. The size of the retinal image may be ascertained by determining the distance of the two lines from each other, and the distance of the lines from the eye, or, from the corresponding visual angle, which is generally from 60 to 90 seconds.

Perimetry.—In order to test **indirect vision**, we may use a **perimeter**. The eye is placed opposite a fixed point, from which a quadrant proceeds, so that the eye lies in the centre of it. As the quadrant rotates round the fixed point, on rotating the former we can circumscribe the surface of a hemisphere, in the centre

Fig. 687.

M'Hardy's perimeter. I, porcelain button; M, bit; E, for fixing the head; *g*, *h*, quadrant; *o*, fixation point; *p*, pointer for piercing the record chart held in the frame (*e*) which moves on *c*; D, upright supporting the quadrant and the automatic arrangement of slides (*k* and *l*), which are moved by *j*.

of which the eye is placed. Proceeding from the fixed point, objects are placed upon semicircles, and are gradually pushed more and more towards the periphery of the field of vision, until the object becomes indistinct, and finally disappears. The process of testing is continued by placing the arc successively in the different meridians of the field of vision.

[M'Hardy's perimeter is a very convenient form (fig. 687). It consists of two uprights (C and D), which are fixed to the opposite ends of a flat basal plate (A). C carries an arrangement for supporting the patient's head, while D carries the automatic arrangement for the perimetric record. Both of these can be raised or depressed by the screws (G and *b*). The patient's chin rests on the chin-rest (E), while in the mouth is placed Landolt's biting fixation (L), which is detachable. The position of the head can be altered by sliding F on L, which can be fixed in any position by the screw (O). The porcelain button (I) just below the patient's eye (*l*) is connected with the adjustment of the "fixation point." The automatic recording apparatus consists of a revolving quadrant (*h*, *h*), which describes a hemisphere round a horizontal axis

passing through the centre of the hollow male axle, turning in the female end of a, which is supported by D. The quadrant can be fixed at any point by g. On the front concave surface of the quadrant is fixed a circular white piece of ivory, representing the "fixation point," from which a needle projects and which is the zero of the instrument. A carriage (i), in which the test objects are placed, can be moved in the concave face of the quadrant by means of the milled head (j), which moves the carriage by means of a tooth and pinion wheel.]

[When the milled head (j) is turned, it moves the carriage and two slides (k and l), the two slides moving in the ratio of 2 to 1. The rate of the carriage is so adjusted that it travels ten times faster than l, and five times faster than k. The pointer (p) is connected with these slides, so that it moves when they move, and records its movements by piercing the record chart, which is fixed in the double-faced frame (e). The frame for the record chart is hinged near c to the upright (D). The frame, when upright, comes so near the pointer that the latter can pierce a chart placed in the frame. The patient is directed to look at the "fixation point," which is merely a small ivory button placed in the imaginary axis of the hemisphere on the front of the centre of the concave surface of the quadrant; the projecting needle-point (o) indicates its position. This is the zero of the quadrant, and on each side of it the quadrant is divided into 90°.]

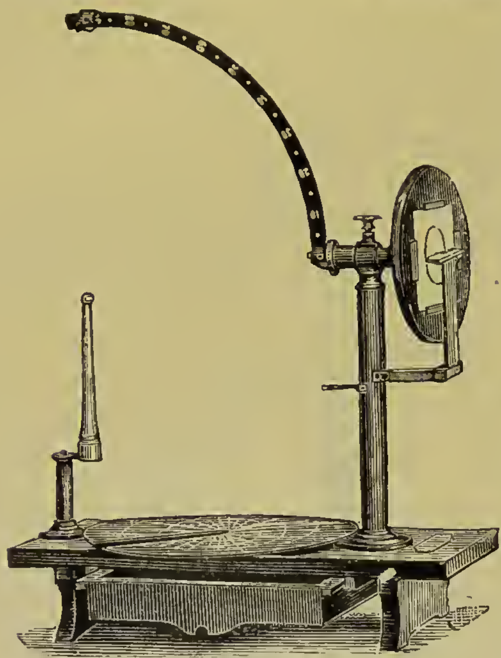


Fig. 688.—Priestley Smith's perimeter.

Fig. 689.

Perimetric chart of a healthy and a diseased eye.

[In testing the field of vision, place the carriage so as to cover zero, adjust the eye for the

fixation point, and look steadily at it, when, if all is right, the pointer (p) ought to pierce the centre of the chart. Move the carriage along the quadrant by j until it disappears from the field of vision, and when it does so the pointer is made to pierce the chart. Make another observation in another direction by altering the position of the quadrant, and go on doing so until a complete record is obtained of the field of vision. Test the other eye in the same way. The colour-field may be tested by using coloured papers in the carriage.]

[**Priestley Smith's Perimeter** (fig. 688).—The wooden knob on the left of the figure is placed under the eye of the patient, who stares at the fixed point in the axis of the quadrant, which can be moved in any meridian. The test object is a square piece of white paper, which is moved along the quadrant. The chart is placed on the posterior surface of the hand-wheel and moves with it, so that the meridians of the chart move with the quadrant. There is a scale behind the hand-wheel corresponding with the circles on the chart, so that the observer can prick off his observations directly.]

[**Scotoma** is the term applied to dimness or blindness in certain parts of the field of vision, which may be **central, marginal,** or **in patches.**]

The capacity for **distinguishing colours** diminishes more rapidly at the periphery of the retina than that for distinguishing differences in the brightness or intensity of light. In fact, the periphery of the retina is slightly red blind. The diminution is greater in the vertical meridian of the eye than in the horizontal, and it diminishes with the distance from the fixation point (*Aubert and Förster*). These observers also state that, during accommodation for a distant object, the diminution of the capacity to distinguish brightness and colour towards the periphery of the lens, occurs more rapidly than with near vision. The excitability of the retina for colours and brightness is greater at a point equally distant from the fovea centralis on the temporal than on the nasal side of the eye (*Schön*).

Perimetric Chart.—If the arc of the perimeter (fig. 688) be divided into 90 degrees, beginning at the fixation point (central point), and proceeding to L and M (fig. 689); and if a series of concentric circles be inscribed on this, with the point of fixation as their centre, we can construct a **topographical chart** of the visual capacity of the normal or healthy eye from the data obtained by the examination of the retina.

Fig. 689 is an example; the *thick* lines indicate a diseased eye, the corresponding *thin* lines a healthy eye. The continuous line indicates the limits for the perception of white; the interrupted line that for blue; the punctuated and interrupted line that for red; m is the blind spot. In the normal eye the limits for the perception of colours are as under:—

	White.	Blue.	Red.	Green.
Externally, ...	70°–88°	65°	60°	40°
Internally, ...	50°–60°	60°	50°	40°
Upwards, ...	45°–55°	45°	40°	30°–35°
Downwards, ...	65°–70°	60°	50°	35°

V. **Specific Energy.**—The rods and cones alone are endowed with what Johannes Müller called "*specific energy,*" *i.e.,* they alone are set into activity by the ethereal vibrations, to produce those impulses which result in vision. *Mechanical* and *electrical* stimuli, however, when applied to any part of the course of the nervous apparatus, produce visual phenomena. Mechanical stimuli are more intense stimuli than light rays, as is shown by performing the dark pressure figure with the eyes open (§ 393, 5, *a*), whereby the circulation in the retina is interfered with; in the region of pressure, we cannot see external objects which affect the retina uniformly and continuously.

VI. The **duration** of the retinal **stimulation** must be exceedingly short, as the electrical spark lasts only 0·000000868 second; still, as a general rule, a shorter time is required, the larger and brighter the object looked at. Alternate stimulation with light, 17 to 18 times per minute, is perceived most intensely (*Brücke*). An interval of 0·027 seconds must elapse between two flashes of light in order that both may be seen separately (*Charpentier*). Further, an increase or diminution of 0·01 part of the intensity of the light is perceptible (§ 383). A shorter time is required to perceive yellow than is required for violet and red (*Vierordt*). The retina becomes more sensitive to light after a person has been kept in the dark for a long time, and also after repose during the night. If light be allowed to act on the eyes for a long time, and especially if it be intense, it causes **fatigue** of the

retina, which begins sooner in the centre than in the periphery of the organ (*Aubert*). At first the fatigue comes on rapidly and afterwards develops more slowly—it is most marked in the morning (*A. Fick*).

VII. During direct vision, objects must traverse at an angular velocity of 1–2 minutes per second in order to appear to be in motion (*Aubert*).

VIII. Visual Purple.—The mode of the action of light upon the end-organs of the retina has already been referred to (p. 915) in connection with the "*visual purple*" or **rhodopsin** (*Boll, Kühne*). Kühne showed that, by illuminating the retina actual pictures (*e.g.*, the image of a window) could be produced on the retina, but they gradually disappeared. From this point of view we might regard the retina as comparable, to a certain extent, to the sensitive plate of a photographic apparatus.

Optogram.—The visual purple is formed by the pigment-epithelium of the retina. Perhaps we might compare the process to a kind of secretion. The visual purple may be restored in a retina by laying the latter upon living choroidal epithelium. The pigment disappears from the mammalian retina by the action of light 60 times more rapidly than from the retina of the frog. In a rabbit's eye, whose pupil was dilated with atropin, Ewald and Kühne obtained a sharp picture or optogram of a bright object placed at a distance of 24 cm. from the eye—the image was "fixed" by a 4 per cent. solution of alum. Visual purple withstands all the oxidising reagents; zinc chloride, acetic acid, and corrosive sublimate change it into a yellow substance —it becomes *white* only through the action of light; the dark heat-rays are without effect, while it is decomposed above a temperature of 52° C. [As visual purple is absent from the cones, and as cones only are present in the fovea centralis, we cannot explain vision by optograms formed by the visual purple.].

Movements of rods and cones.—The inner limb of the cones under the action of light becomes shorter, and elongates in darkness. The action occurs in both eyes, even when the light acts only on one eye. After destruction of the brain, the effect is confined to the eye directly acted on by light. Strychnine tetanus acts like light. It would seem, therefore, that the optic nerve, in addition to afferent light-exciting fibres, contains also motor fibres—retino-motor fibres, according to Engelmann and Stort. Angelucci has observed movements in the outer limbs, and Gradenigo in the inner limbs of the rods. Heat is said to act in a manner similar to light. The isolated inner limbs of the cones exhibit changes of form when acted on by light (*Gradenigo*).

IX. Destruction of the **rods and cones** of the retina causes corresponding dark spots in the field of vision.

396. PERCEPTION OF COLOURS.—Physical.—The vibrations of the light-ether are perceived by the retina only within distinct limits. If a beam of white light, *e.g.*, from the sun, be transmitted through a prism, the light rays are refracted and dispersed, and a "**prismatic spectrum**" is obtained (fig. 23). [If a beam of white light be transmitted through a hole in a shutter into a dark room, and a prism be held in the course of the beam behind the shutter, and in the position shown in fig. 690, then a spectrum or band of colours will be obtained on a white screen placed several feet from the prism. The colours will be in the definite order shown in the diagram; *i.e.*, in order from the least refrangible red to the most refrangible violet. Thus white light contains rays of very different wave-lengths or periods of vibration].

The dark **heat-rays**, or ultra-red rays, whose wave-length is 0·00194 mm., are refracted least, do not act upon the retina, and are therefore invisible. They act, however, upon sensory nerves, and give rise to the sensation of heat. About 90 per cent. of these rays is absorbed by the media of the eye (*Brücke and Knoblauch*). From Fraunhofer's line, A, onwards, the oscillations of the light-ether excite the retina in the following order, and constitute the **visible spectrum** (fig. 690):—**Red** with 481 billions of vibrations per second, **orange** with 532, **yellow** with 563, **green** with 607, **blue** with 653, **indigo** with 676, and **violet** with 764 billion

vibrations per second. The **sensation of colour** therefore depends on the **number of vibrations of the light-ether**, just as the pitch of a note depends on the number of vibrations of the sounding body (*Newton*, 1704; *Hartley*, 1772). Beyond the violet lie the **chemically active ultra-violet** or **actinic rays** of the spectrum. After cutting out all the spectrum, including the violet-rays, v. Helmholtz succeeded in seeing the ultra-violet rays, which had a feeble greyish-blue colour. The heat-rays in the coloured part of the spectrum are transmitted by the media of the eye in the same way as through water. The existence of the ultra-violet rays is best ascertained by the phenomenon of **fluorescence**. Von Helmholtz, on illuminating a solution of sulphate of quinine with the ultra-violet rays, saw a bluish-white light proceeding from all parts of the solution which were acted on by the ultra-violet rays. As the media of the eye themselves exhibit fluorescence (*v. Helmholtz*), they must increase the power of the retina to distinguish these rays. The ultra-violet rays are not largely absorbed by the media of the eye (*Brücke*).

In order that a colour be perceived, it is essential that a certain amount of light fall upon the retina. Blue, when at the lowest degree of brightness, gives a colour sensation with an amount of light which is sixteen times less than that required for red (*Dobrowolsky*).

Intensity of the Impression of Light.—While light of different periods of vibration applied to the eye excites the different sensations of colour, the **amplitude** of the vibrations (height of the waves) determines the **intensity** of the **impression** of light; just as the loudness of a note depends on the amplitude of the vibrations of the sounding body. The sun's light contains all the rays which excite the sensation of colour in us, and when all these rays fall simultaneously upon the retina we experience the sensation of white. If the colours of the spectrum obtained by means of a prism be reunited, white light is again obtained. If no vibrations of the light-ether reach the retina, every sensation of light and colour is absent, but we can scarcely apply the term **black** to this condition. It is rather the **absence of sensation**, such as, for example, is the case when a beam of light falls on the skin of the back. This does not give the sensation of black, but rather that of no sensation of light.

Simple and Mixed Colours.—We distinguish **simple colours**, *e.g.*, those of the spectrum. In order to perceive these, the retina must be excited (set into vibration) by a distinct number of oscillations (see above). Further, we distinguish "**mixed colours**," whose sensations are produced when the retina is excited by two or more simple colours, simultaneously or rapidly alternating. The most complex mixed colour is **white**, which is composed of a mixture of **all the simple** colours of the spectrum.

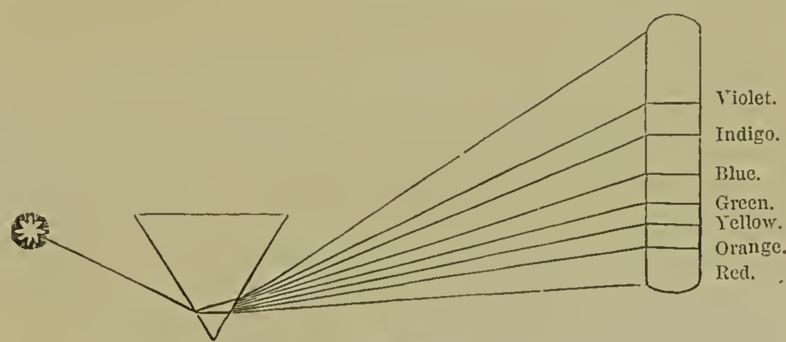


Fig. 690.
Spectrum obtained by means of a prism.

The "**complementary colours**" are important. Any two colours which together give the sensation of white are complementary to each other. The "**contrast colours**" are mentioned here merely to complete the list. They are closely related to the complementary colours. Any two colours which, when mixed, supplement the generally prevailing tone of the light, are contrast colours. When the sky is blue, the two contrast colours must be bluish-white; with bright gaslight they must be yellowish-white, and in pure white light of course all the complementary are the same as the contrast colours (*Brücke*).

Methods of Mixing Colours.—1. Two solar spectra are projected upon a screen, and the spectra are so arranged as to cause any one part of one spectrum to cover any part of the other. 2. Look obliquely through a vertically arranged glass plate at a colour placed behind it.

Another colour is placed in *front* of the glass plate, so that its image is also reflected into the eye of the observer; thus, the light of one colour transmitted through the glass plate and the reflected light from the other colour reach the eye simultaneously. [**Lambert's Method.**—This is easily done by Lambert's method. Use coloured wafers and a slip of glass; place a red wafer on a sheet of black paper, and about 3 inches behind it another blue one. Hold the plate of glass midway and vertically between them, and so incline the glass that, while looking through it at the red wafer, a reflected image of the blue one will be projected into the eye in the same direction as that of the red image, when we have the sensation of purple.]

3. A rotatory disc, with sectors of various colours, is rapidly rotated in front of the eyes. On rapidly rotating the coloured disc, the impressions produced by the individual colours are united to produce a mixed colour. If the rotating disc, which yields, let us suppose, white, on mixing the colours of the spectrum, be reflected in a rapidly rotating mirror, then the individual components of the white reappear.

4. Place in front of each of the small holes in the cardboard used for Scheiner's experiment (fig. 664) two differently coloured pieces of glass; the coloured rays of light passing through the holes unite on the retina, and produce a mixed colour (*Czermak*).

Complementary Colours.—Investigation shows that the following colours of the spectrum are complementary, *i.e.*, every pair gives rise to white :—

Red and greenish-blue,	Orange and cyan-blue,
Yellow and indigo-blue,	Greenish-yellow and violet,

while green has the compound complementary colour, purple (*v. Helmholtz*).

The **mixed colours** may be determined from the following table. At the top of the vertical and horizontal columns are placed the simple colours; the mixed colours occur where they intersect the corresponding vertical and horizontal columns (Dk. = dark; wh. = whitish) :—

	Violet.	Indigo.	Cyan-blue.	Bluish-green.	Green.	Greenish-yellow.	Yellow.
Red	Purple	Dk.-rose	Wh.-rose	White	Wh.-yellow	Gold-yellow	Orange
Orange	Dk.-rose	Wh.-rose	White	Wh.-yellow	Yellow	Yellow	...
Yellow	Wh.-rose	White	Wh.-green	Wh.-yellow	Gr.-yellow	...	...
Gr.-yellow	White	Wh.-green	Wh-green	Green	...	...	...
Green	White-blue	Water-blue	Bl.-green	...	...	...	...
Bluish-green	Water-blue	Water-blue	...	...	...	...	...
Cyan-blue	Indigo	...	...	...	...	...	...

The following **results** have been obtained from observations on the **mixture of colours** :—

1. If two simple, but non-complementary, spectral colours be mixed with each other, they give rise to a colour sensation, which may be represented by a colour lying in the spectrum between both, and mixed with a certain quantity of white. Hence we may produce every impression of mixed colours by a colour of the spectrum + white (*Grassman*).

2. The less white the colours contain, the more "**saturated**" they are said to be; the more white they contain, the more unsaturated do they appear. The saturation of a colour diminishes with the intensity of the illumination.

Geometrical Colour Table.—Since the time of Newton, attempts have been made to construct a so-called "geometrical colour table," which will enable any mixed colour to be readily found. Fig. 691 shows such a colour table; white is placed in the middle, and from it to every point in the curve,—which is marked with the names of the colours,—suppose each colour to be so placed that, proceeding from white, the colours are arranged, beginning with the brightest tone, always followed by the most saturated tone, until the pure saturated spectral colour lies in the point of the curve marked with the name of the colour. The mixed colour, purple, is placed between violet and red. In order to determine from this table the mixed colour of any two spectral colours, unite the points of these colours by a straight line. Suppose weights corresponding to the units of intensity of these colours to be placed on both points of the curve indicating colours, then the position of the centre of gravity of both in the line connecting the colours indicates the position of the mixed colour in the table. The mixed colour of two spectral colours always lies in the colour table in the straight line connecting the two colour points. Further, the impression of the mixed colour corresponds to an intermediate spectral colour mixed with white. The complementary colour of any spectral colour is found at once by making a line from the point of this colour through white, until it intersects the opposite margin of the colour table; the point of intersection indicates the complementary colour. If pure white be produced by mixing

two complementary colours, the colour lying nearest white on the connecting line must be specially strong, as then only would the centre of gravity of the lines uniting both colours lie in the point marked white.

By means of the colour table we may ascertain the *mixed colour of three* or *more colours.* For example, it is required to find the mixed colour resulting from the union of the point, *a* (pale yellow), *b* (fairly saturated bluish-green), and *c* (fairly saturated blue). On the three points place weights corresponding to their intensities, and ascertain the centre of gravity of the weight, *a*, *b*, *c*; it will lie at *p*. It is obvious, however, that the impression of this mixed colour, whitish green-blue, can be produced by green-blue + white, so that *p* may be also the centre of gravity of two weights, which lie in the line connecting white and green-blue.

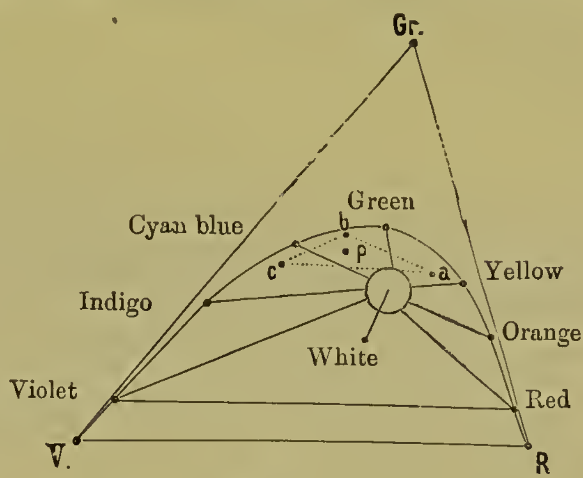


Fig. 691.
Geometrical colour cone or table.

We may describe a triangle, V, Gr. R, about the colour table so as to enclose it completely. The three fundamental or primary colours lie in the angles of this triangle, red, green, violet. It is evident that each of the coloured impressions, *i.e.*, any point of the colour table, may be determined by placing weights corresponding to the intensity of the *primary colours* at the angles of the triangle, so that the point of the colour table, or what is the same thing, the desired mixed colour, is the centre of gravity of the triangle with its angles weighted as above. The intensity of the three primary colours, in order to produce the mixed colour, must be represented in the same proportion as the weights.

Theories of Colour Visions.—Various theories have been proposed to account for colour sensation.

1. According to one theory, colour sensation is produced by *one* kind of element present in the retina, being excited in *different ways* by light of different colours (oscillations of the light ether of different wave-lengths, number of vibrations, and refractive indices).

2. **Young-Helmholtz Theory.**—The theory of Thomas Young (1807) and v. Helmholtz (1852) assumes that **three** different kinds of **nerve-elements**, corresponding to the three primary colours, are present in the retina. Stimulation of the first kind causes the sensation of **red,** of the second **green,** and of the third **violet.**

The elements sensitive to red are most strongly excited by light with the longest wave-length, the red rays; those for green by medium wave-lengths, green rays;

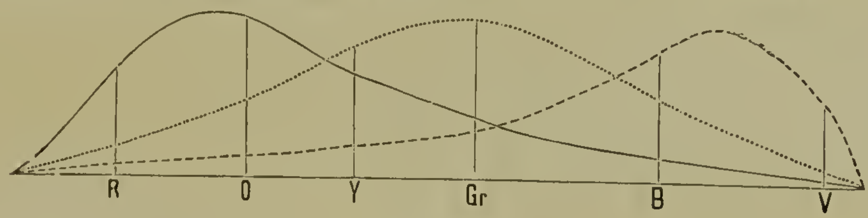


Fig. 692.

those for violet by the rays of shortest wave-length, violet rays. Further, it is assumed, in order to explain a number of phenomena, that *every colour of the spectrum excites all the kinds of fibres, some of them feebly, others strongly.*

Suppose in fig. 692 the colours of the spectrum are arranged in their natural order from red to violet horizontally, then the three curves raised upon the abscissa might indicate the strength of the stimulation of the three kinds of retinal elements. The continuous curve corresponds to the rays producing the sensation of red, the dotted line that of green, and the broken line that of violet. Pure *red* light, as indicated by the height of the ordinates in R, strongly excites the elements sensitive to red, and feebly the other two kinds of terminations,

resulting in the sensation of *red*. Simple yellow excites moderately the elements for red and green, and feebly those for violet=sensation of *yellow*. Simple green excites strongly the elements for green, but much more feebly the other two kinds=sensation of *green*. Simple blue excites to a moderate extent the elements for green and violet; more feebly those for red=sensation of *blue*. Simple violet excites strongly the corresponding elements, feebly the others=sensation of *violet*. Stimulation of any two elements excites the impression of a mixed colour; while, if all of them be excited in a nearly equal degree, the sensation of white is produced. As a matter of fact, the Young-Helmholtz theory gives a simple explanation of the phenomena of the physiological doctrine of colour. It has been attempted to make the results obtained by examination of the structure of the retina accord with this view. According to Max Schultze, the cones alone are end-organs connected with the perception of colour. The presence of longitudinal striation in their outer segments is regarded as constituting them multiple terminal end-organs. Our power of colour [sensation, so far as it depends on the retina, would, on this view of the matter, bear a relation to the number of cones. The degree of colour sensation is most developed in the macula lutea, which contains only cones, and diminishes as the distance from the point increases, while it is absent in the peripheral parts of the retina. The rods of the retina are said to be concerned only with the capacity to distinguish between quantitative sensations of light.

3. **Hering's Theory.**—Ew. Hering, in order to explain the sensation of light proceeds from the axiom stated under 1, p. 955. What we are conscious of, and call a visual sensation, is the psychical expression for the **metabolism in the visual substance** ("*Sehsubstanz*"), *i.e.*, in those nerve-masses which are excited in the process of vision. Like every other corporeal matter, this substance during the activity of the metabolic process undergoes decomposition or "**disassimilation**"; while during rest it must be again renewed, or "**assimilate**" new material. Hering assumes that for the perception of **white** and **black**, two different qualities of the chemical processes take place in the visual substance, so that the sensation of **white** corresponds to the **disassimilation** (decomposition), and that of **black** to the **assimilation** (restitution) of the visual substance.

According to this view, the different degrees of distinctness or intensity with which these two sensations appear, occur in the several transitions between pure white and deep black; or, the proportions in which they appear to be mixed (grey) correspond to the intensity of these two psycho-physical processes. Thus, the consumption and restitution of matter in the visual substance are the primary processes in the sensation of white and black. In the production of the sensation of white, the consumption of the visual substance is caused by the vibrating ethereal waves acting as the discharging force or stimulus, while the degree of the sensation of whiteness is proportional to the quantity of the matter consumed. The process of restitution discharges the sensation of black; the more rapidly it occurs, the stronger is the sensation of black. *The consumption of the visual substance at one place causes a greater restitution in the adjoining parts.* Both processes influence each other simultaneously and conjointly. [In the production of a visual sensation, it is important to remember that the condition of one part of the retina influences contemporaneously the condition of adjoining parts of the retina, *i.e.*, "the sensation which arises through the stimulation of any given point of the retina, is also a function of the state of other immediately contiguous points."] This explains physiologically the phenomenon of **contrast** of which the old view could give only a psychical interpretation (p. 961).

Similarly, **colour sensation** is regarded as a sensation of decomposition (disassimilation) and of restitution (assimilation); in addition to **white**, **red** and **yellow** are the expression of **decomposition**; while **green** and **blue** represent the sensation of **restitution**. Thus, the visual substance is subject to three different ways of chemical change or metabolism. We may explain in this way the *coloured* phenomena of contrast and the complementary after-images. The sensation of black-white may occur simultaneously with all colours; hence, every colour sensation is accompanied by that of dark or bright, so that we cannot have an absolutely pure colour. There are three different constituents of the visual substance; that connected with the sensation of black-white (colourless), that with blue-yellow, and that with red-green. All the rays of the visible spectrum act in disassimilating the black-white substance, but the different rays act in different degrees. The blue-yellow or the red-green substances, on the other hand, are disassimilated only by certain rays, some rays causing assimilation, whilst others are inactive. Mixed light appears colourless when it causes an equally strong disassimilation and assimilation in the blue-yellow and in the red-green substance, so that the two processes mutually antagonise each other, and the action on the black-white substance appears pure. Two objective kinds of light, which together yield white, are not to be regarded as complementary, but as antagonistic, kinds of light, as they do not supplement each other to produce white, but only allow this to appear pure, because, being antagonistic, they mutually prevent each other's action.

The imperfection of the Young-Helmholtz theory of colour sensation is that it recognises only one kind of excitability, excitement, and fatigue (corresponding to Hering's disassimilation), and that it ignores the antagonistic relation of certain light rays to the eye. It does not regard white as consisting of complementary light rays, which neutralise each other by their action on the coloured visual substance, but as uniting to form white (*Hering*).

[While it suffices to explain a great many of the phenomena of light and colour, *e.g.*, the mixing of colours and complementary colours, it does not satisfactorily explain contrast or colour-blindness. Fick admits that it does not explain the following important fact:—Every ray of light, while exciting a colour sensation if it falls on a sufficient area of the posterior polar part of the eyeball, provided it acts on an extremely limited part of the retina, even if it be coloured light, produces a whitish impression. This is exactly the opposite of what we should expect, viz., the smaller the area of retina acted on, the more readily should the particular nerve-ending be excited and a pure colour sensation result.]

In **applying this theory to colour-blindness** (§ 397), we must assume that those who are **red-blind** want the red-green visual substance; there are but two partial spectra in their solar spectrum, the black-white and the yellow-blue. The position of green appears to such an one to be colourless; the rays of the red part of the spectrum are visible, so far as the sensation of yellow and white produced by these rays is strong enough to excite the retina. Hering divides his spectrum into a yellow and a blue half. A **violet-blind** person wants the yellow-blue visual substance; in his spectrum there are only two partial spectra, the black-white and the red-green. In cases of **complete colour-blindness**, the yellow-blue and red-green substances are absent. Hence, such a person has only the sensation of bright and dark. The sensibility to light and the length of the spectrum are retained; the brightest part in this case, as in the normal eye, is in the yellow (*Hering*).

397. COLOUR-BLINDNESS AND ITS PRACTICAL IMPORTANCE.—Causes.—By the term **colour-blindness (dyschromatopsy)** is meant a pathological condition whereby some individuals are unable to distinguish certain colours. Huddart (1777) was acquainted with the condition, but it was first accurately described by Dalton (1794), who himself was red-blind. The term colour-blindness was given to it by Brewster.

The supporters of the Young-Helmholtz theory assume that, corresponding to the paralysis of the three colour-perceiving elements of the retina, there are the following kinds of colour-blindness:—

1. **Red-blindness.** 2. **Green-blindness.** 3. **Violet-blindness.**

The highest degree being termed **complete colour-blindness.**

The supporters of E. Hering's theory of colour sensation distinguish the following kinds:—

1. **Complete Colour-blindness (Achromatopsy).**—The spectrum appears achromatic; the position of the greenish-yellow is the brightest, while it is darker on both sides of it. A coloured picture appears like a photograph or an engraving. Occasionally the different degrees of light intensity are perceived in one shade of colour, *e.g.*, yellow, which cannot be compared with any other colour. O. Becker and v. Hippel observed cases of *unilateral* congenital complete colour-blindness, whilst the other eye was normal for colour-perception.

2. **Blue-yellow Blindness.**—The spectrum is dichromatic, and consists only of red and green. The blue-violet end of the spectrum is usually greatly shortened. In pure cases only the red and green are correctly distinguished (Mauthner's **erythrochloropy**), but not the other colours. Unilateral cases have been observed.

3. **Red-green Blindness.**—The spectrum is also dichromatic. Yellow and blue are correctly distinguished; violet and blue are both taken for blue. The sensations for red and green are absent altogether. There are several forms of this—(*a*) **Green-blindness**, or the red-green blindness, with undiminished spectrum (Mauthner's **xanthokyanopy**), in which bright-green and dark-red are confounded. In the spectrum yellow abuts directly on blue, or between the two, at most, there is a strip of grey. The maximum of brightness is in the yellow. It is often unilateral and often hereditary. (*b*) **Red-blindness** (or the red-green blindness with undiminished spectrum, also called **Daltonism**), in which bright-red and dark-green are confounded. The spectrum consists of yellow and blue, but the yellow lies in the orange. The red end of the spectrum is uncoloured, or even dark. The greatest brightness, as well as the limit between yellow and blue, lies more towards the right.

4. **Incomplete colour-blindness**, or a diminished colour sense, indicates the condition in

which the acuteness of colour perception is diminished, so that the colours can be detected only in large objects, or only when they are near, and when they are mixed with white, they no longer appear as such. A certain degree of this form is frequent, in as far as many persons are unable to distinguish greenish-blue from bluish-green.

Acquired colour-blindness occurs in diseases of the retina and atrophy of the optic nerve in commencing tabes, in some forms of cerebral disease (§ 378, IV. 1), and intoxication. At first green-blindness occurs, which is soon followed by red-blindness. The peripheral zone of the retina suffers sooner than the central area. In hysterical persons there may be intermittent attacks of colour-blindness (*Charcot*) ; and the same occurs in hypnotised persons (p. 848).

H. Cohn found that, on **heating the eyeball** of some colour-blind persons, the colour-blindness disappeared temporarily. Occasionally in persons without a lens red vision is present, and is due to unknown causes. **Percentage.**—Holmgren found that 2·7 per cent. of persons were colour-blind, most being *red* and *green* blind, and very few violet blind.

Limits of Normal Colour-blindness.—The investigations on the power of colour-perception in the *normal* retina are best carried out by means of Aubert-Förster's perimeter, or that of M'Hardy (§ 395). It is found that *our colour perception is complete only in the middle of the field of vision.* Around this is a middle zone, in which only blue and yellow are perceived, in which, therefore, there is red-blindness. Outside this zone, there is a peripheral girdle, where there is complete colour-blindness (§ 395). Hence a red-blind person is distinguished from a person with normal vision, in that the central area of the normal field of vision is absent in the former, this being rather included in the middle zone. The field of vision of a green-blind person differs from that of a person with normal vision, in that his peripheral zone corresponds to the intermediate and peripheral zones of the normal eye. The violet-blind person is distinguished by the complete absence of the normal peripheral zone. The incomplete colour-blindness of these two kinds is characterised by a uniformly diminished central field. [When very intense colours are used, such as those of the solar spectrum, the retina can distinguish them quite up to its margin (*Landolt*).]

In poisoning with **santonin**, violet-blindness (yellow vision) occurs in consequence of the paralysis of the violet perceptive retinal elements, which not unfrequently is preceded by stimulation of these elements, resulting in violet vision, *i.e.*, objects seem to be coloured violet (*Hüfner*). Such is the explanation of this phenomenon given by Holmgren. Max Schultze, however, referred the yellow vision, *i.e.*, seeing objects yellow, to an increase of the yellow pigment in the macula lutea.

When coloured objects are very small, and illuminated only for a short time, the normal eye first fails to perceive red (*Aubert*) ; hence, it appears that a stronger stimulus is required to excite the sensation of red. Brücke found that very rapidly intermittent white light is perceived as green, because the short duration of the stimulation fails to excite the elements of the retina connected with the sensation of red.

[The **practical importance** of colour-blindness was pointed out by George Wilson, and again more recently by Holmgren.] No person should be employed in the marine or railway service until he has been properly certified as able to distinguish red from green.

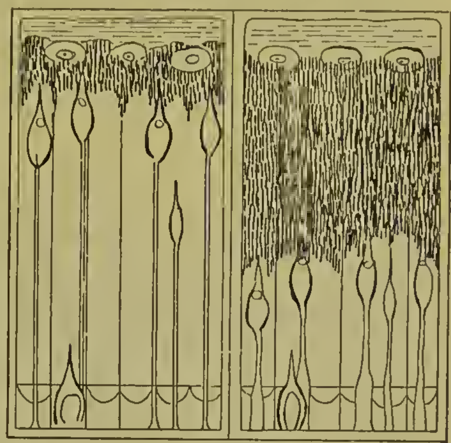
Methods of Testing Colour-blindness.—Following Seebeck, Holmgren used small **skeins of coloured wools** as the simplest material, in red, orange, yellow, greenish-yellow, green, greenish blue, blue, violet, purple, rose, brown, grey. There are five finely graduated shades of each of the above colours. When testing a person, select only one skein—*e.g.*, a bright green or rose—from the mass of coloured wools placed in front of him, and place it aside, asking him to seek out those skeins which he supposes are nearest to it in colour.

Macé and Nacati have measured the acuteness of vision by illuminating a small object with different parts of the spectrum. They compared the observations on red- and green-blind persons with their own results, and found that a red-blind person perceives green light as much brighter than it appears to a normal person. The green-blind had an excessive sensibility for red and violet. It appears that what the colour-blind lose in perceptive power for one colour they gain for another. They have also a keen sense for variations in brightness.

398. STIMULATION OF THE RETINA.—As with every other nervous apparatus, a certain very short but still determinable time elapses after the rays of light fall upon the eye before the action of the light takes place, whether the light acts so as to produce a conscious impression, or produces merely a reflex effect upon the pupil. The *strength* of the impression produced depends partly and chiefly upon the excitability of the retina and the other nervous structures. If the light acts for a long time with equal intensity, the excitation, after having reached its culminating point, rapidly diminishes again, at first more rapidly, and afterwards more and more slowly.

[When the **retina is stimulated by light**, there is (1) an effect on the rhodopsin (p. 915). (2) The electro-motive force is diminished (§ 332). (3) The processes

of the hexagonal pigment-cells of the retina dipping between the rods and cones are affected; thus they are retracted in darkness, and protruded in the light (fig. 693). (4) Engelmann has shown that the length and shape of the cones vary with the action of light (p. 952). The cones are retracted in darkness and protruded under the influence of light (fig. 693). This alteration in the shape of the cones takes place even if the light acts on the skin, and not on the eyeball at all.]



1. Fig. 693. 2.

The cones of the retina and pigment-cells (of the frog) as affected by light and darkness: 1, after two days in darkness; 2, after ten minutes in daylight.

After-Images.—If the light acts on the eye for some time so as to excite the retina, and if it be suddenly withheld, the retina still remains for some time in an excited condition, which is more intense and lasts longer, the stronger and the longer the light may have been applied, and the more excitable the condition of the retina. Thus, after every visual perception, especially if it is very distinct and bright, there remains a so-called "**after-image.**" We distinguish a "**positive after-image,**" which is an image of similar brightness, and a similar colour.

"That the impression of any picture remains for some time upon the eye is a physiological phenomena; when such an impression can be seen for a long time, it becomes pathological. The weaker the eye is, the longer the image remains upon it. The retina does not recover itself so quickly, and we may regard the action as a kind of paralysis. This is not to be wondered at in the case of dazzling pictures. After looking at the sun, the image may remain on the retina for several days. A similar result sometimes occurs with pictures which are not dazzling. Busch records that the impression of an engraving, with all its details, remained on his eye for 17 minutes" (*Goethe*).

Experiments and Apparatus for Positive After-Images.—1. When a burning stick is rapidly rotated, it appears as a fiery circle.

2. The **Phanakistoscope** (*Plateau*) or the **stroboscopic discs** (*Stampfer*). Upon a disc or cylinder, a series of objects is so depicted that successive drawings represent individual factors of one continuous movement. On looking through an opening at such a disc rotated rapidly, we see pictures of the different phases moving so quickly that each rapidly follows the one in front of it. As the impression of the one picture remains until the following one takes its place, it has the appearance as if the successive phases of the movement were continuous, and one and the same figure. The apparatus under the name of **zoetrope**, which is extensively used as a toy, is generally stated to have been invented in 1832. It was described by Cardanus in 1550. It may be used to represent certain movements, *e.g.*, of the spermatozoa and ciliary motion, the movements of the heart and those of locomotion.

3. The **colour top** contains on the sectors of its disc the colours which are to be mixed. As the colour of each sector leaves a condition of excitation for the whole duration of a revolution, all the colours must be perceived simultaneously, *i.e.*, as a mixed colour.

[**Illusions of Motion.**—Silvanus P. Thompson points out that if a series of concentric circles in black and white be made on paper, and the sheet on which the circles are drawn be moved with a motion as if one were rinsing out a pail, but with a very minute radius, then all the circles appear to rotate with the same angular velocity as that imparted. Professor Thompson has contrived other forms of this illusion, in the form of **strobic discs.**]

Negative After-Images.—Occasionally, when the stimulation of the retina is strong and very intense, a "negative," instead of a positive after-image, appears. In a negative after-image, the *bright* parts of the object appear *dark*, and the *coloured* parts in corresponding **contrast colours** (p. 961).

Examples of Negative After-Images.—After looking for a long time at a dazzlingly-illuminated white window, on closing the eyes we have the impression of a bright cross, or crosses, as the case may be, with dark panes.

Negative coloured after-images are beautifully shown by Nörrenberg's apparatus. Look steadily at a coloured surface, *e.g.*, a yellow board with a small blue square attached to the

centre of its surface. A white screen is allowed to fall suddenly in front of the board—the white surface now has a bluish appearance, with a yellow square in its centre.

The usual explanation of dark negative after-images is that the retinal elements are fatigued by the light, so that for some time they become less excitable, and consequently light is but feebly perceived in the corresponding areas of the retina; hence, darkness prevails.

Hering explains the dark after-images as due to a process of assimilation in the black-white visual substance. In explaining *coloured* after-images, the Young-Helmholtz theory assumes that, under the action of the light waves, *e.g.*, red, the retinal elements connected with the perception of this colour are paralysed. On now looking suddenly on a white surface, the mixture of all the colours appears as white *minus* red, *i.e.*, the white appears *green*. In bright daylight the contrast colour lies very near the complementary colour. According to Hering, the contrast after-image is explained by the assimilation of the corresponding coloured visual substance, in this case, of the "red-green" (§ 397). From the commencement of a momentary illumination until the appearance of an after-image, 0·344 sec. elapses (*v. Vintschgau and Lustig*).

Not unfrequently, after intense stimulation of the retina, positive and negative after images *alternate* with each other until they gradually fuse. After looking at the dark-red setting sun we see alternately discs of red and green.

The phenomena of contrast undergo some modification in the peripheral areas of the retina, owing to the partial colour-blindness which occurs in these areas (*Adamück and Woinow*).

Irradiation is the term applied to certain phenomena where we form a false estimate of visual impressions, owing to *inexact accommodation*. If, from inexact accommodation, the margins of the object are projected upon the retina in diffusion circles, the mind tends to add the undefined margin to those parts of the visual image which are most prominent in the image itself. What is *bright* appears larger and overcomes what is dark, while an object, without reference to brightness or colour, has the same relation to its background (fig. 694). When the accommodation is quite accurate, the phenomenon of irradiation is not present. [On looking at fig. 695 from a distance, the white squares appear larger and as if they were united by a white band.]

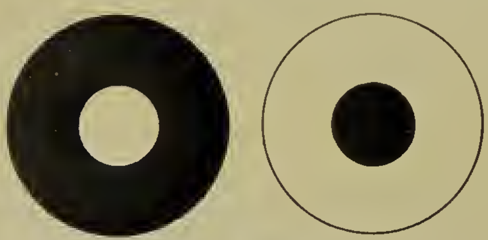


Fig. 694.
For irradiation.

Fig. 695.
For irradiation.

"A dark object appears smaller than a bright one of the same size. On looking at the same time from a certain distance at two circles of the same size, a white one on a black background, and a black on a white background, we estimate the latter to be about one-fifth less than the former (fig. 694). On making the black circle one-fifth larger they will appear equal. Tycho de Brahe remarks that the moon, when in conjunction (dark), appears to be one-fifth smaller than in opposition (full, bright). The first lunar crescent appears to belong to a larger disc than the dark one adjoining it, which can occasionally be distinguished at the time of the new light. Black clothes make persons appear to be much smaller than light clothes. A light seen behind a margin gives the appearance of a cut in the margin. A ruler, behind which is placed a lighted candle, appears to the observer to have a notch in it. The sun, when rising and setting, appears to make a depression in the horizon" (*Goethe*).

[**Contrast.**—The fundamental phenomena are such as these, that a bright object looks brighter surrounded by objects darker than itself; and darker with surroundings brighter than itself. There may be contrasts either with bright or dark objects or with coloured ones.]

Simultaneous Contrast.—By this term is meant a phenomenon like the following:—When *bright* and *dark* parts are present in a picture at the same time, the bright (white) parts always appear to be more intensely bright the less white there is near them, or, what is the same thing, the darker the surroundings, and, conversely, they appear less bright the more white tints that are present near them. A similar phenomenon occurs with *coloured* pictures. A colour in a picture appears to us to be more intense the less of this colour there is in the adjoining parts, that is, the more the surroundings resemble the tints of the contrast colour. Simultaneous contrast arises from simultaneous impressions occurring in two adjoining and different parts of the retina.

Examples of Contrast for Bright and Dark.—1. Look at a white network on a black ground; the parts where the white lines intersect appear darker, because there is least black near them.

2. Look at a point of a small strip of dark grey paper in front of a dark black background. Push a large piece of white paper between the strip and the background; the strip on the white ground now appears to be much darker than before. On again removing the white paper, the strip at once again appears bright (*Hering*).

3. Look with both eyes towards a greyish-white surface, *e.g.*, the ceiling of a room. After gazing for some time, place in front of the eye a paper tube eight inches long, and an inch to an inch and a quarter in diameter, blackened in the inside. The part of the ceiling seen through the tube appears as a round white spot (*Landois*).

Examples for colours.—1. Place a piece of grey paper on a red, yellow, or blue ground; the contrast colours appear at once, viz., green, blue, or yellow. The phenomenon is made still more distinct by covering the whole with transparent tracing paper (*Herm. Meyer*). Under similar circumstances, printed matter on a coloured ground appears in its complementary colour (*W. v. Bezold*).

2. An air-bubble in the strongly tinged field of vision of a thick microscopical preparation appears with an intense contrast colour (*Landois*).

3. Paste four green sectors upon a rotatory white disc, leave a ring round the centre of the disc uncovered by green, and cover it with a black strip. On rotating such a disc the black part appears red and not grey (*Brücke*).

4. Look with both eyes towards a greyish-white surface, and place in front of one eye a tube about the length and breadth of a finger, composed of transparent oiled paper, gummed together to such thickness as will permit light to pass through its walls. The part of the surface seen through the tube appears in its contrast colour. The experiment also shows the contrast in the intensity of the illumination (*Landois*). A white piece of paper, with a round black spot in its centre, when looked at through a blue glass, appears blue with a black spot. If a white spot of the same size on a black ground be placed in front, so that it is reflected in the glass plate and just covers the black spot, it shows the contrast colour yellow (*Ragona Scina*).

5. The **coloured shadows** also belong to the group of simultaneous contrasts. "Two conditions are necessary for the production of coloured shadows—firstly, that the light gives some kind of a colour to the white surface; second, that the shadow is illuminated, to a certain extent, by another light. During the twilight, place a short lighted candle on a white surface, between it and the fading daylight hold a pencil vertically, so that the shadow thrown by the candle is illuminated, but not abolished, by the feeble daylight; the shadow appears of a beautiful *blue*. The blue shadow is easily seen, but it requires a little attention to observe that the white paper acts like a reddish-yellow surface, whereby the blue colour apparent to the eye is improved. One of the most beautiful cases of coloured shadows is seen in connection with the full moon. The light of the candle and that of the moon can be completely equalised. Both shadows can be obtained of equal strength and distinctness, so that both colours are completely balanced. Place the plate opposite the light of the moon, the lighted candle a little to one side at a suitable distance. In front of the plate hold an opaque body, when a double shadow appears, the one thrown by the moon and lighted by the candle being bright reddish-yellow; and, conversely, the one thrown by the candle and lighted by the moon appears of a beautiful blue. Where the two shadows come together and unite is black" (*Goethe*).

6. "Take a plate of green glass of considerable thickness and hold it so as to get the bars of a window reflected in it, the bars will be seen double, the image formed by the under surface of the glass being *green*, while the image coming from the under surface of the glass, and which ought really to be colourless, appears to be purple. The experiment may be performed with a vessel filled with water, with a mirror at its base. With pure water colourless images are obtained, while by colouring the water coloured images are produced" (*Goethe*).

Explanation of Contrast.—Some of these phenomena may be explained as due to an error of judgment. During the simultaneous action of several impressions, the judgment errs, so that when an effect occurs at one place, this acts to the slightest extent in the neighbouring parts.

When, therefore, brightness acts upon a part of the retina, the judgment ascribes the smallest possible action of the brightness to the adjoining parts of the retina. It is the same with colours. It is far more probable that the phenomena are to be referred to actual physiological processes (*Hering*). Partial *stimulation with light affects not only the parts so acted on but also the surrounding area of the retina* (p. 956); the part directly excited undergoing increased *dis-assimilation*, the (indirectly stimulated) adjoining area undergoing increased *assimilation*; the increase of the latter is greatest in the immediate neighbourhood of the illuminated portion, and rapidly diminishes as the distance from it increases. By the increase of the assimilation in those parts not acted on by the image of the object, this is prevented, so that the diffused light is perceived. The increase of the assimilation in the immediate neighbourhood of the illuminated spot is greatest, so that the perception of this relatively stronger different light is largely rendered impossible (*Hering*).

[Helmholtz thus ascribed the phenomena of contrast to psychical conditions, *i.e.*, errors of judgment, but this explanation is certainly not complete. A far more satisfactory solution of the problem is that of Hering, that stimulation of one part of the retina affects the condition of adjoining parts. If a white disc on a black background be looked at for a time, and then the eyes be closed, a negative after-image of the disc appears, but it is darker and blacker than the visual area, and it has a light area around, brightest close to the disc, *i.e.*, the adjacent part of the retina is affected. This Hering has called **successive light induction.**]

Successive Contrast.—Look for a long time at a dark or bright object, or at a coloured (*e.g.*, red) one, and then allow the effect of the contrast to occur on the retina, *i.e.*, with reference to the above, bright and dark, or the contrast colour green, then these become very intense. This phenomenon has also been called "*successive contrast.*" In this case the negative after-image obviously plays a part.

[Some **drugs** cause subjective visual sensations, but these do so by acting on the brain, *e.g.*, alcohol, as in delirium tremens, cannabis indica, sodic salicylate, and large doses of digitalis (*Brunton*).]

399. MOVEMENTS OF THE EYEBALLS—EYE MUSCLES.—The globular eyeball is capable of extensive and free movement on the correspondingly excavated fatty pad of the orbit, just like the head of a long bone in the corresponding socket of a freely movable arthroidal joint. The movements of the eyeball, however, are limited by certain conditions, by the mode in which the eye-muscles are attached to it. Thus, when one muscle contracts, its antagonistic muscle acts like a bridle, and so limits the movement; the movements are also limited by the insertion of the optic nerve. The soft elastic pad of the orbit on which the eyeball rests is itself subject to be moved forward or backward, so that the eyeball also must participate in these movements.

Protrusion of the eyeball takes place—1. By congestion of the blood-vessels, especially of the veins in the orbit, such as occurs when the outflow of the venous blood from the head is interfered with, as in cases of hanging. 2. By contraction of the smooth muscular fibres in Tenon's capsule, in the spheno-maxillary fissure, and in the eyelids (§ 404), which are innervated by the cervical sympathetic nerve. 3. By voluntary forced opening of the palpebral fissure, whereby the pressure of the eyelids acting on the eyeball is diminished. 4. By the action of the oblique muscles, which act by pulling the eyeball inwards and forwards. If the superior oblique be contracted when the eyelids are forcibly opened, the eyeball may be protruded about 1 mm. When protrusion of the eyeball occurs pathologically (as in 1 and 2), the condition is called **exophthalmos.**

Retraction of the eyeball is the opposite condition, and is caused—1. By closing the eyelids forcibly. 2. By an empty condition of the retrobulbar blood-vessels, diminished succulence, or disappearance of the tissue of the orbit. 3. Section of the cervical sympathetic in dogs causes the eyeball to sink somewhat in the orbit. The smooth muscular fibres of Tenon's capsule are perhaps antagonistic in their action to the four recti when acting together, and thus prevent the eyeball from being drawn too far backwards. Many animals have a special *retractor bulbi* muscle, *e.g.*, amphibians, reptiles, and many mammals; the ruminants have four.

The movements of the eyes are almost always accompanied by similar movements of the head, chiefly on looking upwards, less so on looking laterally, and least of all when looking downwards.

The difficult investigations on the movements of the eyeballs have been carried out, especially by Listing, Meissner, Helmholtz, Donders, A. Fick, and E. Hering.

Axes.—All the movements of the eyeball take place round its **point of rotation**

(fig. 696, O), which lies 1·77 mm. behind the centre of the visual axis, or 10·957 mm. from the vertex of the cornea (*Donders*). In order to determine more carefully the movements of the eyeball, it is necessary to have certain definite data :—1. The **visual axis** (S, S_1), or the antero-posterior axis of the eyeball, unites the point of rotation with the fovea centralis, and is continued straight forwards to the vertex of the cornea. 2. The **transverse**, or **horizontal axis** (Q, Q_1), is the straight line connecting the points of rotation of both eyes and its extension outwards. Of course, it is at right angles to 1. 3. The **vertical axis** passes vertically through the point of rotation at right angles to 1 and 2. These three axes form a co-ordinate system. We must imagine that in the orbit there is a fixed determinate axial system, whose point of intersection corresponds with the point of rotation of the eyeball. When the eye is at rest (primary position), the three axes of the eyeball completely coincide with the three axes of the co-ordinate system in the orbit. When the eyeball however is moved, two or more axes are displaced from this, so that they must form angles with the fixed orbital system.

Planes of Separation.—In order to be more exact, and also partly for further estimations, let us suppose three *planes* passing through the eyeball, and that their position is secured by any two axes. 1. The **horizontal** plane of separation divides the eyeball into an upper and lower half; it is determined by the visual transverse axis. In its course through the retina it forms the **horizontal line of separation** of the latter; the coats of the eyeball itself cut it in their horizontal meridian. 2. The **vertical** plane divides the eyeball into an inner and outer half; it is determined by the visual and vertical axes. It cuts the retina in the **vertical line of separation** of the latter and the periphery of the bulb in the vertical meridian of the eyeball. 3. The **equatorial** plane divides the eyeball into an anterior and posterior half; its position is determined by the vertical and transverse axes, and it cuts the sclerotic in the equator of the eyeball. The horizontal and vertical lines of separation of the retina, which intersect in the fovea centralis, divide the retina into four quadrants.

In order to define more precisely the movements of the eyeball, v. Helmholtz has introduced the following terms :—He calls the straight line which connects the point of rotation of the eye with the fixed point in the outer world, the **visual line** ("Blicklinie"), while a plane passing through these lines in both eyes he called the *visual plane*; the *ground line* of this plane is the line uniting the two points of rotation, viz., the transverse axis of the eyeball. Suppose a sagittal section (antero-posterior) to be made through the head, so as to divide the latter into a right and left half, then this plane would halve the ground line of the visual plane, and when prolonged forward would intersect the visual plane in the median line. The visual point of the eye can be (1) raised or lowered—the field which it traverses being called the visual field ("Blickfeld"); it is part of a spherical surface with the point of rotation of the eye in its centre. Proceeding from the primary position of both eyes, which is characterised by both visual lines being parallel with each other and horizontal, then the elevation of the visual plane can be determined by the angle which this forms with the plane of the primary position. This angle is called the *angle of elevation*—it is positive when the visual plane is raised (to the forehead), and negative when it is lowered (chinwards). (2) From the primary position, the visual line can be turned laterally in the visual plane. The extent of this lateral deviation is measured by the **angle of lateral rotation**, *i.e.*, by the angle which the visual line forms with the median line of the visual plane; it is said to be positive when the posterior part of the visual line is turned to the right, negative when to the left. The following are the positions of the eyeball :—

1. **Primary position** [or "position of rest"], in which both the lines of vision are parallel with each other, and the visual planes are horizontal. The three axes of the eyeball coincide with the three fixed axes of the co-ordinate system in the orbit.

2. **Secondary positions** are due to movements of the eye from the primary position. There are two different varieties—(*a*) where the visual lines are parallel, but are directed *upwards* or *downwards*. The transverse axis of both eyes remains the same as in the primary position; the deviations of the other two axes expressed

by the amount of the angle of elevation of the line of vision. (*b*) The second variety of the secondary position is produced by the *convergence* or *divergence* of the lines of vision. In this variety the vertical axis, round which the lateral rotation takes place, remains as in the primary position; the other axes form angles; the amount of the deviation is expressed by the "angle of lateral rotation." The eye, when in the primary position, can be rotated from this position 42° outwards, 45° inwards, 34° upwards, and 57° downwards (*Schuurmann*).

3. **Tertiary position** is the position brought about by the movements of the eye, in which the lines of vision are *convergent*, and are at the same time *inclined* upwards or downwards.

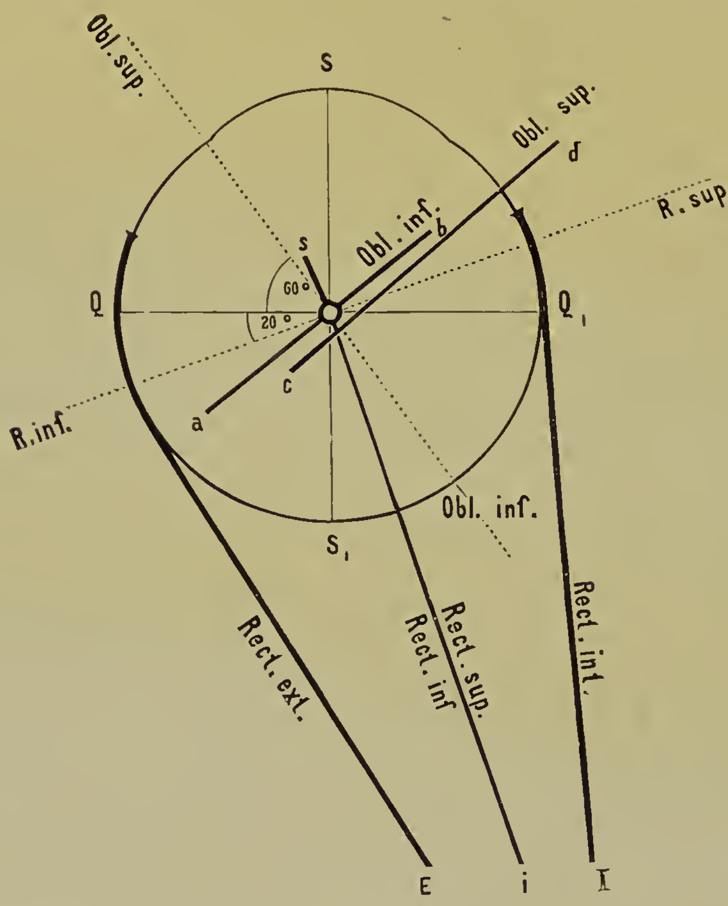


Fig. 696.

Scheme of the action of the ocular muscles.

[Listing's Law is that which expresses the movements of the eyeball. When the eyeball moves from the primary position, or position of rest, the angle of rotation of the eye in the second position is the same as if the eye were turned about a fixed axis perpendicular to both the first and the second positions of the visual line (*Helmholtz*).]

All the three axes of the eye are no longer coincident with the axes in the primary position. The exact direction of the visual lines is determined by the amount of the angle of lateral rotation and the angle of elevation. There is still another important point. The eyeball is always rotated at the same time round the line of vision and round its axis (*Volkmann*, *Hering*). As the iris rotates round the visual line like a wheel round its axis, this rotation is called "circular rotation"

(" *Raddrehung* ") of the eye, which is always connected with the tertiary positions. Even oblique movements may be regarded as composed of—(1) a rotation round the vertical axis, and (2) round the transverse axis; or it may be referred to rotation round a single constant axis placed between the above-named axes, passing through the point of rotation of the eyeball, and at right angles to the secondary and primary direction of the visual axis (line of vision)—(*Listing*). The amount of circular rotation is measured by the angle which the horizontal separation line of the retina forms with the horizontal separation of the retina of the eye in the primary position. This angle is said to be positive, when the eye itself rotates in the same direction as the hand of a watch observed by the same eye, *i.e.*, when the upper end of the vertical line of separation of the retina is turned to the right.

According to Donders, the angle of rotation increases with the angle of elevation and the angle of lateral rotation—it may exceed 10°. With equally great elevation or depression of the visual plane, the rotation is greater, the greater the elevation or depression of the line of vision.

On looking *upwards* in the tertiary position, the upper ends of the vertical lines of separation of the retina *diverge*; on looking downwards they converge. If the visual plane be raised, the eye, when it deviates laterally to the right, makes a circular rotation to the left. When the visual plane is depressed, on deviating the eye to the right or left, there is a corresponding circular rotation to the right or left. Or we may express the result thus:—When the angle of elevation and the angle of deviation have the same sign (+ or −), then the rotation of the eyeball is negative; when, however, the signs are unequal, the rotation is positive. In order to make the circular rotation visible in one's own eye, accommodate one eye for a surface divided by vertical and horizontal lines until a positive after-image is produced, and then rapidly rotate the eye into the third position. The lines of the after-image then form angles with the lines of the background. As the position of the vertical meridian of the eye is important from a practical point of view, it is necessary to note that, in the primary and secondary positions of the eyes, the vertical meridian retains its vertical position. On looking to the left and upwards, or to the right and downwards, the vertical meridians of both eyes are turned to the left; conversely, they are turned to the right on looking to the left and downwards, or to the right and upwards.

In the secondary positions of the eye, rotation of the axis of the eye never occurs (*Listing*). Very slight rolling of the eyes occurs, however, when the head is inclined towards the shoulder, and in the direction opposite to that of the head; it is about 1° for every 10° of inclination of the head (*Skrebitzk*).

Ocular Muscles.—The movements of the eyeball are accomplished by means of the **four straight** and **two oblique** ocular muscles (fig. 697). In order to understand the action of each of these muscles, we must know the plane of traction of the muscles and the axis of rotation of the eyeball. The **plane of traction** is found by the plane lying in the middle of the origin and insertion of the muscle and the point of rotation of the eyeball. The **axis of rotation** is always at right angles to the plane of traction in the point of rotation of the eyeball.

1. The **rectus internus** (I) and **externus** (E) rotate the eye almost exactly inwards and outwards (fig. 696). The plane of traction lies in the plane of the paper; Q, E, is the direction of the traction of the external rectus; Q_1, I, that of the internal. The axis of rotation is in the point of rotation, O, at right angles to the plane of the paper, so that it coincides with the vertical axis of the eyeball. 2. The axis of rotation of the **R. superior** and **inferior** (the dotted line, R. sup., R. inf.), lies in the horizontal plane of separation of the eye, but it forms an angle of about 20° with the transverse axis (Q, Q_1); the direction of the traction for both muscles is indicated by the line, *s*, *i*. By the action of these muscles, the cornea is turned upwards and slightly inwards, or downwards and slightly inwards. 3. The axis of rotation of both oblique muscles (the dotted lines, Obl. sup. and Obl. inf.) also lies in the horizontal plane of separation of the eyeball, and it forms an angle of 60° with the transverse axis. The direction of the traction of the *inferior* oblique gives the line, *a*, *b*; that of the *superior*, the line, *c*, *d*. The action of these muscles, therefore, is in the one case to rotate the cornea outwards and upwards, and in the other outwards and downwards. These actions, of course, only

obtain when the eyes are in the primary position—in every other position the axis of rotation of each muscle changes.

When the eyes are at rest, the muscles are in equilibrium. Owing to the power of the internal recti, the visual axes converge and would meet, if prolonged 40 centimetres in front of the eye. In the movements of the eyeball, one, two, or three muscles may be concerned. **One muscle** acts only when the eye is moved directly outwards or inwards, especially the internal and external rectus. **Two muscles** act when the eyeball is moved directly upwards (superior rectus and

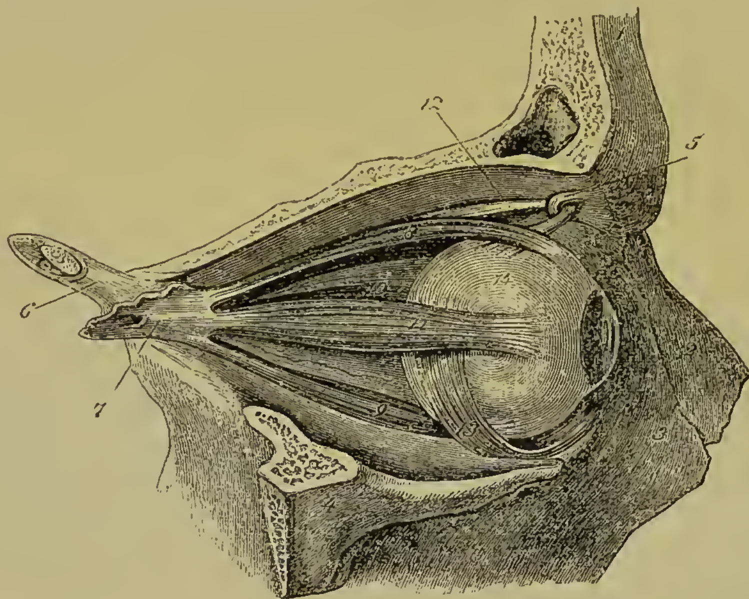


Fig. 697.

Lateral view of the muscles of the eyeball. 5, Trochlea or pulley of the superior oblique muscle, 12. 6, Optic nerve. 8, Superior, 9, inferior, and 12, external rectus. 13, Inferior oblique.

inferior oblique) or downwards (inferior rectus and superior oblique). **Three muscles** are in action when the eyeballs take a diagonal direction, especially for *inwards* and *upwards*, by the internal and the superior rectus and inferior oblique; for *inwards* and *downwards*, the internal and inferior rectus and superior oblique; for *outwards* and *downwards*, the external and inferior rectus and superior oblique; for *outwards* and *upwards*, the external and superior rectus and inferior oblique.

[The following table shows the action of the muscles of the eyeball :—

Inwards, .	Rectus internus.	*Inwards and downwards*,	Rectus internus. Rectus inferior. Obliquus superior.
Outwards, .	Rectus externus.		
Upwards, .	Rectus superior. Obliquus inferior.	*Outwards and upwards*,	Rectus externus. Rectus superior. Obliquus inferior.
Downwards, .	Rectus inferior. Obliquus superior.		
Inwards and upwards,	Rectus internus. Rectus superior. Obliquus inferior.	*Outwards and downwards*,	Rectus externus. Rectus inferior. Obliquus superior.

Ruete imitated the movements of the eyeballs by means of a model, which he called the **ophthalmotrope**.

The extent of the movements of the eyeball and its length diminish with age. The mobility is less in the vertical than in the lateral direction, and less upwards than downwards. The normal and myopic eye can be moved more outwards, and the long-sighted eye more inwards, the external and internal recti act most when the eye is moved outwards, the oblique when it is rotated inwards. An eye can be turned inwards to a greater extent when the other eye at

the same time is turned outwards than when the other is turned inwards. During near vision, the right eye can be turned less to the right, and the left to the left, than during distant vision (*Hering*).

Simultaneous Ocular Movements.—Both eyes are always moved simultaneously. Even when one eye is quite blind, the ocular muscles move when the whole eyeball is excited. When the head is straight, the movements always take place so that both visual planes (visual axes) lie in the same plane. In front both visual axes can diverge only to a trifling extent, while they can converge considerably. If individual ocular muscles are paralysed, the position of the visual axis in the same plane is disturbed, and *squinting* results, so that the patient no longer can direct both visual axes simultaneously to the same point, but he directs the one eye after the other. Even nystagmus (p. 893) occurs in both eyes simultaneously, and in the same direction. The innate simultaneous movement of both eyes is spoken of as an **associated movement** (*Joh. Müller*). E. Hering showed that in all ocular movements there is a *uniformity of the innervation* as well. Even during such movements in which one eye apparently is at rest, there is a movement, due to the action of two antagonistic forces, the movements resulting in a slight to and fro motion of the eyeball.

The **motor nerves** of the ocular muscles are the oculomotorius (§ 345), the trochlearis (§ 346), and the abducens (§ 348). The **centre** lies in the corpora quadrigemina, and below it (§ 379), and partly in the medulla oblongata (§ 379).

400. BINOCULAR VISION.—**Advantages.**—Vision with both eyes affords the following advantages:—(1) The *field of vision* of both eyes is considerably larger than that of one eye. (2) The perception of *depth* is rendered easier, as the retinal images are obtained from two different points. (3) A more exact estimate of the *distance* and *size* of an object can be formed, in consequence of the perception of the degree of convergence of both eyes. (4) The *correction of certain errors* in the one eye is rendered possible by the other.

When the position of the head is *fixed*, we can easily form a conception as to the *form of the entire field of vision* if we close one eye and direct the open eye inwards. We observe that it is pear-shaped, broad above and smaller below, the silhouette, or profile of the nose, causes the depression between the upper and lower part of the field.

401. IDENTICAL POINTS—HOROPTER.—**Identical points.**—If we imagine the retinæ of both eyes to be a pair of hollow saucers placed one within the other, so that the yellow spots of both eyes coincide, and also the similar quadrants of the retinæ, then all those points of both retinæ which coincide or cover each other are called "**identical**" or "**corresponding points**" of the retina. The two meridians which separate the quadrants coinciding with each other are called the "**lines of separation.**" Physiologically, the identical points are characterised by the fact that, when they are both simultaneously excited by light, the excitement proceeding from them is, by a psychical act, referred to one and the same point of the field of vision, lying, of course, in a direction through the nodal point of each eye. Stimulation of *both* identical points causes only *one* image in the field of vision. Hence all those objects of the external world, whose rays of light pass through the nodal points to fall upon identical points of the retina, are seen *singly*, because their images from both eyes are referred to the same point of the field of vision, so that they cover each other. All other objects whose images do not fall upon identical points of the retina cause **double vision**, or **diplopia.**

Proofs.—If we look at a linear object with the points 1, 2, 3, then the corresponding retinal images are 1, 2, 3, and 1, 2, 3, which are obviously identical points of the retinæ (fig. 698). If, while looking at this line, there be a point, A, nearer the eyes, or B, further from them, then, on focussing for 1, 2, 3, neither the rays (A, *a*, A, *a*) coming from A, nor those (B, *b*, B, *b*) from B, fall upon identical points; hence A and B appear double.

Make a point (*e.g.*, 2) with ink on paper; of course the image will fall upon both foveæ centrales of the retinæ (2, 2), which of course are identical points. Now press laterally upon one

eye, so as to displace it slightly, then two points at once appear, because the image of the point no longer falls upon the fovea centralis of the displaced eye, but on an adjoining non-identical part of the retina. When we squint voluntarily all objects appear double.

The vertical surfaces of separation of the retina do not exactly coincide with the *vertical meridians*. There is a certain amount of divergence (0·5°–3°), less above, which varies in different individuals, and it may be in the same individual at different times (*Hering*). The horizontal lines of separation, however, coincide. Images which fall upon the vertical lines of separation appear to be vertical to those on the horizontal lines, although they are not actually so. Hence, the vertical lines of separation are the *apparent* vertical meridians. Some observers regard the identical points of the retina as an *acquired* arrangement; others regard it as normally *innate*. Persons who have had a squint from their birth see singly; in these cases, the identical points must be differently disposed.

The **horopter** represents all those points of the outer world from which rays of light passing into both eyes fall upon identical points of the retina, the eyes being in a certain position. It varies with the different positions of the eyes.

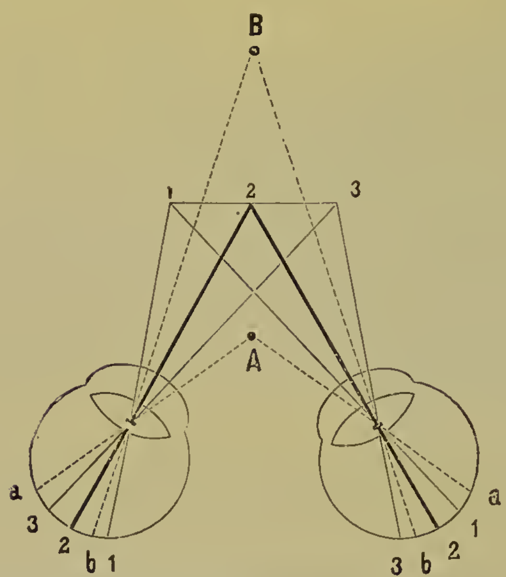


Fig. 698.
Scheme of identical and non-identical points of the retina.

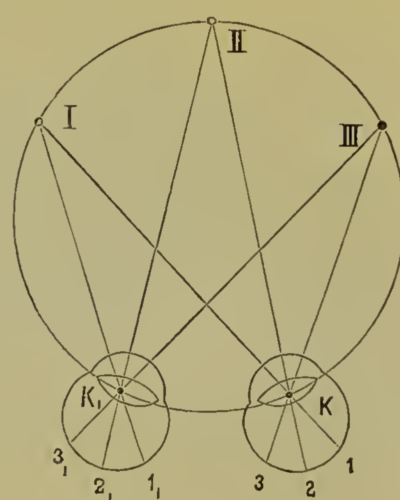


Fig. 699.
Horopter for the secondary position, with convergence of the visual axes.

1. In the **primary position** of both eyes with the visual axes parallel, the rays of direction proceeding from two identical points of the two retinæ are parallel and intersect only at infinity. Hence for the primary position the horopter is a plane in infinity.

2. In the **secondary position** of the eyes with converging visual axes, the horopter for the transverse lines of separation is a circle which passes through the nodal points of both eyes (fig. 699, K, K_1), and through the fixed points I, II, III. The horopter of the vertical lines of separation is in this position vertical to the plane of vision.

3. In the symmetrical **tertiary position**, in which the horizontal and vertical lines of separation form an angle, the horopter of the vertical lines of separation is a straight line inclined towards the horizon. There is no horopter for the identical points of the horizontal lines of separation, as the lines of direction prolonged from the identical points of these points do not intersect.

4. In the unsymmetrical tertiary position (with rolling) of the eyes, in which the fixed point lies at unequal distances from both nodal points, the horopter is a curve of a complex form.

All objects, the rays proceeding from which fall upon **non-identical** points of the retinæ, appear **double**. We can distinguish *direct* or *crossed* double images, according as the rays prolonged from the non-identical points of the retina intersect *in front* of or *behind* the fixed point.

Experiment.—Hold two fingers—the one behind the other—before both eyes. Accommodate for the far one and then the near one appears double, and when we accommodate for the near one the far one appears double. If, when accommodating for the near one, the right eye

be closed, the left (crossed) image of the far finger disappears. On accommodating for the far finger and closing the right eye, the right (direct) double image of the near finger disappears.

Double images are referred to the proper distance from the eyes just as single images are.

Neglect of Double Images.—Notwithstanding the very large number of double images which must be formed during vision, they do not disturb vision. As a general rule, they are "neglected," so that the attention must, as a rule, be directed to them before they are perceived. This condition is favoured thus:—

1. The attention is always directed to the point of the field of vision which is accommodated for at the time. The image of this part is projected on to both yellow spots, which are identical points of the retina.
2. The form and colour of objects on the lateral parts of the retina are not perceived so sharply.
3. The eyes are always accommodated for those points which are looked at. Hence, indistinct images with diffusion circles are always formed by those objects which yield double images, so that they can be more readily neglected.
4. Many double images lie so close together that the greater part of them, when the images are large, covers the other.
5. By practice images which do not exactly coincide may be united.

402. STEREOSCOPIC VISION.—On looking at an object, both eyes do not yield exactly similar images of that object—the images are slightly different,

Fig. 700.
Stereoscopic views of blocks of wood.

because the two eyes look at the object from two different points of view. With the right eye we can see more of the side of the body directed towards it, and the same is the case with the left eye. Fig. 700 shows the appearance of blocks of wood as viewed by the right and left eyes respectively. Notwithstanding this inequality, the two images are united. How two different images are combined is best understood by analysing the stereoscopic images.

Let, in fig. 701, L and R represent two such images as are obtained with the left and right eyes. These images, when seen with a stereoscope, look like a truncated pyramid, which projects towards the eye of the observer, as the points indicated by the same signs cover each other. On measuring the distance of the points, which coincide or cover each other in both figures, we find that the distances A, *a*, B, *b*, C, *c*, D, *d* are equally great, and at the same time are the *widest* of all the points of both figures; the distance E, *e*, F, *f*, G, *g*, H, *h* are also equal, but are *smaller* than the former. On looking at the coinciding lines (A, E, *a*, *e*, and B, F, *b*, *f*), we observe that all the points of this line which lie nearer to A *a* and B *b* are further apart than those lying nearer E *e* and F *f*.

Comparing these results with the stereoscopic image, we have the following laws for **stereoscopic vision**:—1. All those points of two stereoscopic images, and of

course of two retinal images of an object, which in both images are equally distant from each other, appear on the same plane. **2.** All points which are nearer to each other, compared with the distance of other points, appear to be nearer to the observer. **3.** Conversely, all points which lie further apart from each other appear perspectively in the background.

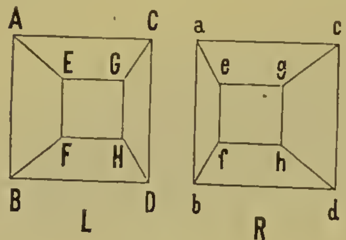


Fig. 701.
Two stereoscopic drawings.

The **cause** of this phenomenon lies in the fact that, "in vision with both eyes we constantly refer the position of the individual images in the direction of the visual axis to where they both intersect."

Proofs.—The following stereoscopic experiment proves this (fig. 703):—Take both images of two pairs of points (a, b, and α, β), which are at unequal distances from each other on the surface of the paper. By means of small stereoscopic prisms cause them to coincide, then the combined point, A of a, and α appears at a distance on the plane of the paper, while the other point, B, produced by the superposition of b and β, floats in the air before the observer. Fig. 703 shows how this occurs. The following experiment shows the same result:—Draw two figures, which are to be superposed similar to the lines B A, A E, b a, and a e, in fig. 701. In the lines B A, and b a, all the points which are to be superposed lie equally distant from each other, while, on the contrary, all the points in A E, and a e, which lie nearer E and e, are constantly nearer to each other. When looked at with a stereoscope, the superposed verticals, A B, and a b, lie in the plane of the paper, while the superposed lines, A E, and a e, project obliquely towards the observer from the plane of the paper. From these two fundamental experiments we may analyse all pairs of stereoscopic pictures. Thus, in fig. 701, if we exchange the two pictures, so that R lies in the place of L, then we must obtain the impression of a truncated hollow pyramid.

Two stereoscopic pictures, which are so constructed that the one contains the body from the front and above, and the other it from the front and below (suppose in fig. 702 the lines A B, and a b, were the ground lines), can never be superposed by means of the stereoscope.

This process has been explained in another way. Of the two figures, R and L (fig. 701), only A B C D, and a b c d, fall upon identical points of the retina, hence

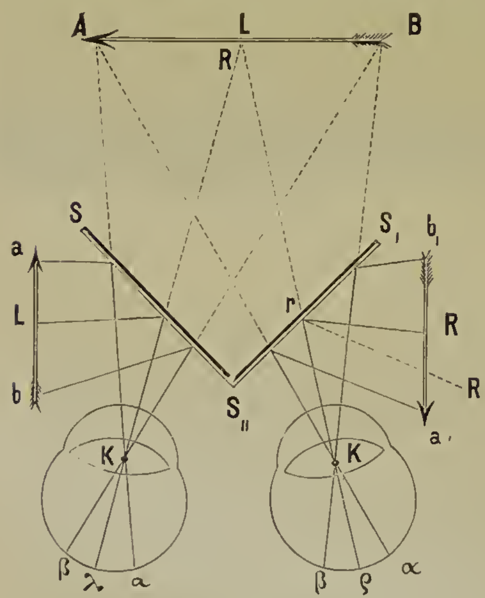


Fig. 702.
Wheatstone's stereoscope.

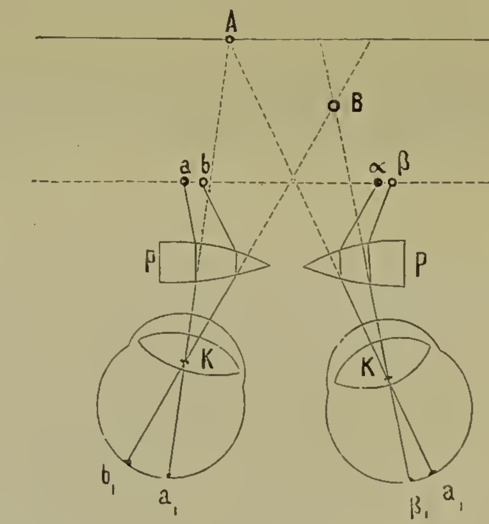


Fig. 703.
Scheme of Brewster's stereoscope.

these alone can be superposed; or, when there is a different convergence of the visual axis, only E F G H, and e f g h, can be superposed for the same reason. Suppose the square ground surfaces of the figures are first superposed, in order to

explain the stereoscopic impression, it is further assumed that both eyes, after superposition of the ground squares, are rapidly moved towards the apex of the pyramid. As the axis of the eyes must thereby converge more and more, the apex of the pyramid appears to project; as all points which require the convergence of the eyes for their vision appear to us to be nearer (see below). Thus, all corresponding parts of both figures would be brought, one after the other, upon identical points of the retina by the movements of the eyes (*Brücke*).

It has been urged against this view that the duration of an electrical spark suffices for stereoscopic vision (*Dove*)—a time which is quite insufficient for the movements of the eyes. Although this may be true for many figures, yet in the correct combination of complex or extraordinary figures, these movements of the visual axes are not excluded, and in many individuals they are distinctly advantageous. Not only the actual movements necessary for this act, but the sensations derived from the muscles are also concerned.

When two figures are *momentarily* combined to form a stereoscopic picture, there being no movement of the eyes, clearly many points in the stereoscopic pictures are superposed which, *strictly* speaking, do not fall upon identical points of the retina. Hence we cannot characterise the identical points of the retina as coinciding mathematically; but from a physiological point of view we must regard such points as identical, which, *as a rule*, by simultaneous stimulation, give rise to a single image. The mind obviously plays a part in this combination of images. There is a certain psychical tendency to fuse the double images on the retinæ into one image, in accordance with the fact that we, from experience, recognise the existence of a single object. If the differences between two stereoscopic pictures be too great, so that parts of the retina too wide apart are excited thereby, or when new lines are present in a picture, and do not admit of a stereoscopic effect, or disturb the combination, then the stereoscopic effect ceases.

The **stereoscope** is an instrument by means of which two somewhat similar pictures drawn in perspective may be superposed so that they appear single. Wheatstone (1838) obtained this result by means of two mirrors placed at an angle (fig. 702); Brewster (1843) by two prisms (fig. 703). The construction and mode of action are obvious from the illustrations.

Some pairs of two such pictures may be combined, without a stereoscope, by directing the visual axis of each eye to the picture held opposite to it.

Two completely identical pictures, *i.e.*, in which all corresponding points have exactly the same relation to each other as the same sides of two copies of a book, appear quite flat under the stereoscope; as soon, however, as in one of them one or more points alters its relation to the corresponding points, this point either projects or recedes from the plane.

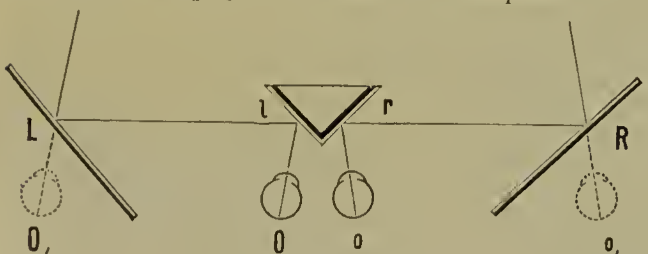


Fig. 704.
Telestereoscope of v. Helmholtz.

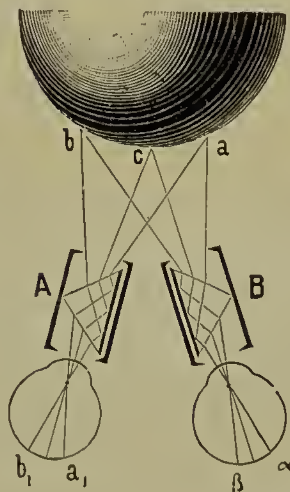


Fig. 705.
Wheatstone's pseudoscope.

Telestereoscope.—When objects, placed at a great distance, are looked at, *e.g.*, the most distant part of a landscape, they appear to us to be flat, as in a picture, and do not stand out, because the slight differences of position of our eyes in the head are not to be compared with the great distance. In order to obtain a stereoscopic view of such objects, v. Helmholtz constructed the **telestereoscope** (fig. 704), an apparatus which by means of two parallel mirrors,

places, as it were, the point of view of both eyes wider apart. Of the mirrors, L and R each projects its image of the landscape upon l and r, to which both eyes, O, o, are directed. According to the distance between L and R, the eyes, O, o, as it were, are displaced to O_1, o_1. The distant landscape appears like a stereoscopic view. In order to see distant parts more clearly and nearer, a double telescope or opera-glass may be placed in front of the eyes.

Take two corresponding stereoscopic pictures, with the surfaces black in one case and light in the other. Draw two truncated pyramids like fig. 701, make one figure exactly like L, *i.e.*, with a white surface and black lines, and the other with white lines and a black surface, then under the stereoscope such objects **glance.** The cause of the glancing condition is that the glancing body at a certain distance reflects bright light into one eye and not into the other, because a ray reflected at an angle cannot enter both eyes simultaneously (*Dove*).

Wheatstone's Pseudoscope consists of two right-angled prisms (fig. 705, A and B) enclosed in a tube, through which we can look in a direction parallel with the surfaces of the hypothenuses. If a spherical surface be looked at with this instrument, the image formed in each eye is inverted laterally. The right eye sees the view usually obtained by the left eye and conversely; the shadow which the body in the light throws upon a light ground is reversed. Hence the ball appears hollow.

Struggle of the Fields of Vision.—The stereoscope is also useful for the following purpose:—In vision with both eyes, both eyes are almost never active simultaneously and to the same extent; both undergo variations, so that first the impression on the one retina and then that on the other is stronger. If two different surfaces be placed in a stereoscope, then, especially when they are luminous, these two alternate in the general field of vision, according as one or other eye is active (*Panum*). Take two surfaces with lines ruled on them, so that when the surfaces are superposed the lines will cross each other, then either the one or the other system of lines is more prominent (*Panum*). The same is true with coloured stereoscopic figures, so that there is a contest or struggle of the coloured fields of vision.

403. ESTIMATION OF SIZE AND DISTANCE.—**Size.**—We estimate the size of an object—apart from all other factors—from the **size of the retinal image**; thus the moon is estimated to be larger than the stars. If, while looking at a distant landscape, a fly should suddenly pass across our field of vision, near to our eye, then the image of the fly, owing to the relatively great size of the retinal image, may give one the impression of an object as large as a bird. If, owing to defective accommodation, the image gives rise to diffusion circles, the size may appear to be even greater. But objects of very unequal size give equally large retinal images, especially if they are placed at such a distance that they form the same **visual angle** (fig. 658); so that in estimating the **actual size** of an object, as opposed to the **apparent size** determined by the visual angle, the *estimate of distance* is of the greatest importance.

As to the **distance** of an object, we obtain some information from the **feeling of accommodation**, as a greater effort of the muscle of accommodation is required for exact vision of a near object than for seeing a distant one. But, as with two objects at unequal distances giving retinal images of the *same size*, we know from experience that that object is smaller which is near, then that object is estimated to be the smaller for which, during vision, we must accommodate more strongly.

In this way we explain the following:—A person beginning to use a microscope always observes with his eyes accommodated for a near object, while one used to the microscope looks through it without accommodating. Hence beginners always estimate microscopic objects as too small, and on making a drawing of them it is too small. If we produce an after-image in one eye, it at once appears smaller on accommodating for a near object, and again becomes larger during negative accommodation. If we look with one eye at a small body placed as near as possible to the eye, then a body lying behind it, but seen only indirectly, appears smaller.

Angle of Convergence of Visual Axes.—In estimating the **size** of an object, and taking into account our estimate of its distance, we also obtain much more important information from the degree of **convergence of the visual axes.** We refer the position of an object, viewed with both eyes, to the point where both visual axes intersect. The angle formed by the two visual axes at this point is called the "angle of convergence of the visual axes" ("*Gesichtswinkel*"). The larger, therefore, the visual angle, the size of the retinal image remaining the same—we judge the object to be nearer. The nearer the object is, it may be the smaller, in order

to form a "**visual angle**" of the same size, such as a distant large object would give. Hence, we conclude, that with the same apparent size (equally large visual angle, or retinal images of the same size) we judge that object to be smallest which gives the greatest convergence of the visual axes during binocular vision. As to the muscular exertion necessary for this purpose, we obtain information from the **muscular sense** of the ocular muscles.

Experiments and Proofs.—The chess-board phenomenon of H. Meyer—1. If we look at a uniform chess-board-like pattern (tapestry or carpet), then, when the visual axes are directed directly forwards, the spaces on the pattern appear of a certain size. If, now, we look at a nearer object, we may cause the visual axes to cross, when the pattern apparently moves towards the plane of the fixed point, so that the crossed double images are superposed, and the pattern at once appears smaller.

2. Rollett looks at an object through two thick prisms of glass placed at an angle. The plates are at one time so placed that the apex of the angle is directed towards the observer (fig. 706, II), at another in the reverse position (I). If both eyes, f and i, are to see the object a, in I, then as the glass plates so displace the rays, a, c, and a, g, as to make them parallel with the direction of these rays, viz., c, f, and h, i, then the eyes must *converge* more than when they are turned directly towards a. Hence the object appears nearer and smaller, as at a. In II, the rays, b_1 k, and b_1 o, from the nearer object b_1, fall upon the glass plates. In order to see b_1, the eyes (n and q) must *diverge* more, so that b appears more distant and larger.

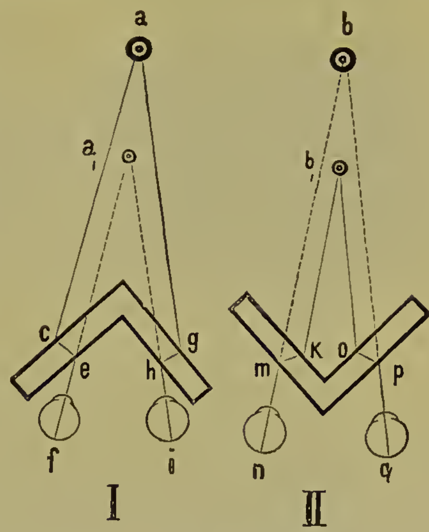


Fig. 706.
Rollett's glass plate apparatus.

3. In looking through *Wheatstone's reflecting stereoscope* (fig. 702), it is obvious that the more the two images approach the observer, the more must the observer converge his visual axes, because the angles of incidence and reflection are greater. Hence the compound picture now appears to him to be *smaller*. If the centre of the image, R, recedes to R_1, then of course the angle, S_{11}, rp, is equal to S_1, rR_1, and the same on the left side.

4. In using the *telestereoscope*, the two eyes are, as it were, separated from each other, then of course in looking at objects at a certain distance the convergence of the visual axes must be greater than in normal vision. Hence, objects in a landscape appear as in a small model. But as we are accustomed to infer that such small objects are at a great distance, hence the objects themselves appear to recede in the distance.

Estimation of Distance.—When the retinal images are of the same size, we estimate the distance to be greater the less the **effort of accommodation**, and conversely. In binocular vision, when the retinal images are of the same size, we infer that that object is most distant for which the optic axes are least converged, and conversely. Thus, the estimation of size and distance go hand in hand, in great part at least, and the correct estimation of the distance also gives us a correct estimate of the size of objects (*Descartes*). A further aid to the estimation of distance is the observation of the *apparent displacement* of objects, on moving our head or body. In the latter, especially, lateral objects appear to change their position toward the background, the nearer they are to us. Hence, when travelling in a train, in which case the change of position of the objects occurs very rapidly, the objects themselves are regarded as nearer, and also smaller (*Dove*). Lastly, those objects appear to us to be *nearest* which are most *distinct* in the field of vision.

Example.—A light in a dark landscape, and a dazzling crown of snow on a hill, appear to be near to us; looked at from the top of a high mountain, the silver glancing curved course of a river not unfrequently appears as if it were raised from the plane.

False Estimates of Size and Direction.—1. A line divided by intermediate points appears longer than one not so divided. Hence the heavens do not appear to us as a hollow sphere,

but as curved like an ellipse; and for the last reason the disc of the setting sun is estimated to be larger than the sun when it is in the zenith. 2. If we move a circle slowly to and fro behind a slit, it appears as a horizontal ellipse; if we move it rapidly, it appears as a vertical ellipse. 3. If a very fine line be drawn obliquely across a vertical thick black line, then the direction of the fine line beyond the thick one appears to be different from its original direction.

4. **Zöllner's Lines.**—Draw three parallel horizontal lines 1 centimetre apart, and through the upper and lower ones draw short oblique parallel lines in the direction from above and the left to below and the right; through the middle line draw similar oblique lines, but in the opposite direction, then the three horizontal lines no longer appear to be parallel. [Fig. 707 shows a modification of this. The lines are actually parallel, although some of them appear to converge and others to diverge.] If we look in a dark room at a bright vertical line, and then bend the head towards the shoulder, the line appears to be bent in the opposite direction (*Aubert*).

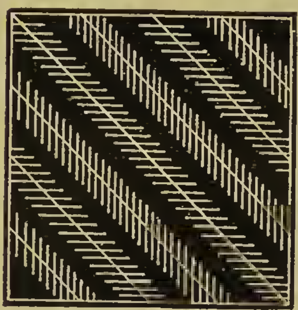


Fig. 707.
Zöllner's lines.

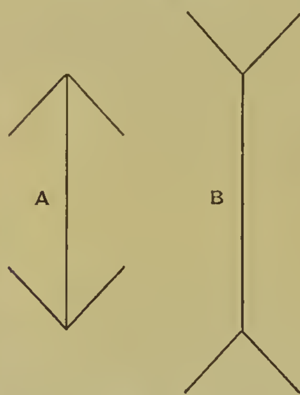


Fig. 708.
To show a false estimate of size.

[5. The length of a line appears to vary according to the angle and direction of certain other lines in relation to it (fig. 708). The length of the vertical lines on the left is the same as that on the right, yet the latter is judged to be the longer.]

404. PROTECTIVE ORGANS OF THE EYE.—I. The **eyelids** are represented in section in fig. 709. The tarsus is in reality not a cartilage, but merely a rigid plate of connective-tissue, in which the **Meibomian glands** are imbedded; acinous sebaceous glands moisten the edges of the eyelids with fatty matter. At the basal margin of the tarsus, especially of the upper one, close to the reflection of the conjunctiva, open the acino-tubular glands of Krause. The conjunctiva covers the anterior surface of the eyeball as far as the margin of the cornea, over which the epithelium alone is continued. On the posterior surface of the eyelid, the conjunctiva is partly provided with papillæ. It is covered by stratified squamous epithelium. Coiled **glands** occur in ruminants just outside the margin of the cornea, while outside this, towards the outer angle of the eye in the pig, there are simple glandular sacs. Waldeyer describes modified sweat-glands in the tarsal margins in man. Small lymphatic sacs in the conjunctiva are called trachoma glands. Krause found **end-bulbs** in the conjunctiva bulbi (§ 424). The blood-vessels in the conjunctiva communicate with the juice-canals in the cornea and sclerotic (p. 907). The secretion moistening the conjunctiva, besides some mucus, consists of tears, which may be as abundant as that formed in the lachrymal glands.

Closure of the eyelids is effected by the orbicularis palpebrarum (*facial nerve*, § 349), whereby the upper lid falls in virtue of its own weight. This muscle contracts—(1) voluntarily; (2) involuntarily (single contractions); (3) reflexly by stimulation of all the sensory fibres of the trigeminus distributed to the eyeball and its immediate neighbourhood (§ 347), also by intense stimulation of the retina by light; (4) continued involuntary closure occurs during sleep.

Opening of the eyelids is brought about by the passive descent of the lower one, and the active elevation of the upper eyelid by the levator palpebræ superioris (§ 345). The smooth muscular fibres of the eyelids also aid (p. 975). In looking downwards, the lower eyelid is pulled downwards by bands of connective-tissue which run from the inferior rectus to the inferior tarsal cartilage (*Schwalbe*).

II. The **lachrymal apparatus** consists of the **lachrymal glands**, which in struc-

ture closely resemble the parotid, their acini being lined by low cylindrical granular epithelium. Four to five larger, and eight to ten smaller **excretory ducts** conduct the tears above the outer angle of the upper lid into the fornix conjunctiva. The **tear ducts**, beginning at the puncta lachrymalis, are composed of connective- and elastic-tissue, and are lined by stratified squamous epithelium. Striped muscle accompanies the duct, and by its contraction keeps the duct open. Toldt found no sphincter surrounding the puncta lachrymalia, while Gerlach found an incomplete circular musculature. The connective-tissue covering of the tear sac and canal is united with the adjoining periosteum. The thin mucous membrane, which contains much adenoid tissue and lymph-cells, is lined by a single layer of ciliated cylindrical epithelium, which below passes into the stratified form. The opening of the duct is often provided with a valve-like fold (Hasner's valve).

The **conduction of the tears** occurs between the lids and the bulb by means of *capillarity*, the closure of the eyelids aiding the process. The Meibomian secretion prevents the overflow of the tears [just as greasing the edge of a glass vessel prevents the water in it from overflowing]. The tears are conducted from the puncta through the duct, chiefly by a siphon action. Horner's muscle (also known to Duverney, 1678] likewise aids, as every time the eyelids are closed it pulls upon the posterior wall of the sac, and thus dilates the latter, so that it aspirates tears into it (*Henke*).

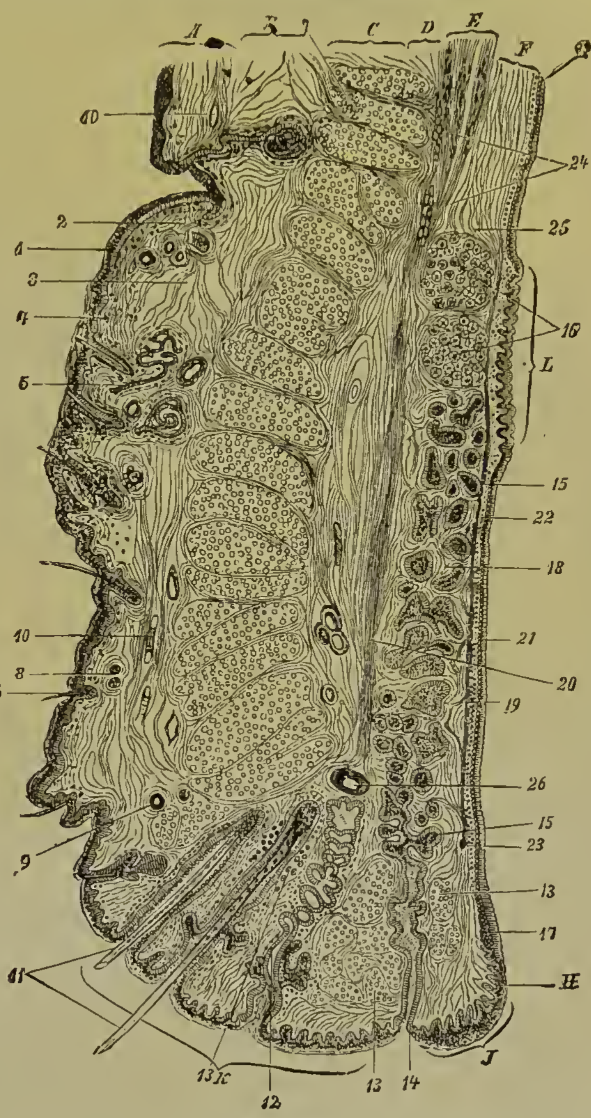


Fig. 709.

Vertical section through the upper eyelid. *A*, cutis, 1, epidermis; 2, chorium; *B* and 3, sub-cutaneous connective-tissue; *C* and 7, orbicularis muscle; *D*, loose sub-muscular connective-tissue; *E*, insertion of H. Müller's muscle; *F*, tarsus; *G*, conjunctiva; *J*, inner, *K*, outer edge of the lid; 4, pigment cells; 5, sweat-glands; 6, hair follicles; 8 and 23, sections of nerves; 9, arteries; 10, veins; 11, cilia; 12, modified sweat-glands; 13, circular muscle of Riolan; 14, Meibomian gland; 15, section of an acinus of the same; 16, posterior tarsal glands; 18 and 19, tissue of the tarsus; 20, pretarsal or sub-muscular connective-tissue; 21 and 22, conjunctiva, with its epithelium; 24, fat; 25, loosely woven posterior end of the tarsus; 26, section of a palpebral artery.

E. H. Weber and Hasner ascribe the aspiration of the tears to the diminution of the amount of air in the nasal cavities during inspiration. Arlt asserts that the tear sac is compressed by the contraction of the orbicularis muscle, so that the tears must be forced towards the nose. Lastly, Stellwag supposes that when the eyelids are closed the tears are simply pressed into the puncta, while Gad denies that there is any kind of pumping mechanism in the nasal canal. Landois points out that

the tear ducts are surrounded by a plexus of veins, which according to their state of distention may influence the size of these tubes.

The **secretion of tears** takes place only by *direct* stimulation of the lachrymal nerve (§ 347, I., 2), subcutaneous malar (§ 347, II., 2), and cervical sympathetic (§ 356, A, 6), which have been called **secretory nerves.** Secretion may also be excited *reflexly* (§ 347, I., 2) by stimulation of the nasal mucous membrane only on the same side (*Herzenstein*). The ordinary secretion in the waking condition is really a reflex secretion produced by the stimulation of the anterior surface of the bulb by the air, or by the evaporation of tears. A very **bright light** also causes a reflex secretion of tears, the optic being the afferent nerve. The **centre** in the rabbit does not extend forward beyond the origin of the fifth nerve, but it extends downwards to the fifth vertebra (*Eckhard*). During sleep all these factors are absent, and there is no secretion. **Histological changes.**—Reichel found that in the **active gland** (after injection of pilocarpin), the secretory cells became granular, turbid, and smaller, while the outlines of the cells became less distinct, and the nuclei spheroidal. In the **resting gland,** the cells are bright and slightly granular with irregular nuclei. Intense stimulation by *light* acting on the optic nerve causes a reflex secretion of tears. The flow of tears accompanying certain violent emotions, and even hearty laughing, is still unexplained. During coughing and vomiting the secretion of tears is increased partly reflexly, and partly by the outflow being prevented by the expiratory pressure.

Function of tears.—The tears moisten the bulb, protect it from drying, and float away small particles, being aided in this by the closure of the eyelids. Atropin diminishes the tears (*Mogaard*).

Composition of tears.—The tears are alkaline, saline to taste, and represent a "serous" secretion. Water 98·1 to 99; 1·46 organic substances (0·1 albumin and mucin, 0·1 epithelium); 0·4 to 0·8 salts (especially NaCl).

[**Action of Drugs.**—Essential volatile oils and eserin increase the secretion of tears, atropin arrests it, while eserin antagonises the effect of atropin and causes an increased secretion.]

405. COMPARATIVE—HISTORICAL.—**Comparative.**—The **simplest form** of visual apparatus is represented by aggregations of pigment-cells in the outer coverings of the body, which are in connection with the termination of afferent nerves. The pigment absorbs the rays of light, and in virtue of the light-ether discharges kinetic energy, which excites the terminations of the nervous apparatus. Collections of pigment-cells, with nerve-fibres attached, and provided with a clear refractive body, occur on the margin of the bell of the higher medusæ, while the lower forms have only aggregations of pigment on the bases of their tentacles. Also in many lower worms there are pigment spots near the brain. In others, the pigment lies as a covering round the terminations of the nerves, which occur as "crystalline rods" or "crystalline spheres." In parasitic worms the visual apparatus is absent. In **star-fishes,** the eyes are at the tips of the arms, and consist of a spherical crystal organ surrounded with pigment, with a nerve going to it. In all other echinodermata there are only accumulations of pigment. Amongst the **annulosa** there are several grades of visual apparatus—(1) **Without a cornea,** there may be only one crystal sphere (nervous end-organ) near the brain, as in the young of the crab; or there may be several crystal spheres forming a compound eye, as in the lower crabs. (2) **With a cornea,** consisting of a lenticular body formed from the chitin of the outer integument, the eye itself may be simple, merely consisting of one crystal rod, or it may be compound. The compound eye consists of only one large lenticular cornea, common to all the crystal rods, as in the spiders; or each crystal rod has a special lenticular cornea for itself. The numerous rods surrounded by pigment are closely packed together, and are arranged upon a curved surface, so that their free ends also form a part of a sphere. The chitinous investment of the head is facetted, and forms a small corneal lens on the free end of each rod. According to one view, each facette, with the lens and the crystal sphere, is a special eye, and just as man has two eyes so insects have several hundred. Each eye sees the picture of the outer world *in toto.* This view is supported by the following experiment of van Leeuwenhoek:—If the cornea be sliced off, each facette thereof gives a special image of an object. If a cross be made on the mirror of a microscope, while a piece of the facetted cornea is placed as an object upon the stage, then we see an image of the cross in each facette of the cornea. Thus for each rod (crystal sphere) there would be a special image. Each corneal facette, however, forms only a part of the image of the outer world, so that we must regard the image as composed like a mosaic. Amongst **mollusca,**

the fixed brachiopoda have two pigment spots near the brain, but only in their larval condition; while the mussel has, under similar conditions, pigment spots with a refractive body. The adult mussel, however, has pigment spots (ocelli) only in the margin of the mantel, but some molluscs have stalked and highly developed eyes. Some of the lower snails have no eyes, some have pigment spots on the head, while the garden snail has stalked eyes provided with a cornea, an optic nerve with retina and pigment, and even a lens and vitreous body. Amongst **cephalopoda**, the nautilus has no cornea or lens, so that the sea-water flows freely into the orbits. Others have a lens and no cornea, while some have an opening in the cornea (Loligo, Sepia, Octopus). All the other parts of the eye are well developed. Amongst **vertebrata**, Amphioxus has no eyes. They exist in a degenerated condition in Proteus and the mammal Spalax. In many fishes, amphibians, and reptiles, the eye is covered by a piece of transparent skin. [**Pineal or Epiphysial Eye.**—Some lizards, *e.g.*, Hatteria, have a rudimentary median eye in the median line of the head, and lodged in the parietal foramen. It is developed from the pineal body, and its lens is formed from the optic cup, so that light falls upon the retina without penetrating the fibres of the optic nerve. Thus, it is an invertebrate type of eye, where the retina and lens are developed from epidermal structures, while in the vertebrate eye, the retina is developed from the cerebrum (fig. 710).] Some hag-fishes, the crocodile, and birds have eyelids, and a **nictitating membrane** at the inner angle of the eye. Connected with it is the **Harderian gland**. In mammals the nictitating membrane is represented only by the plica semilunaris. There is no lachrymal apparatus in fishes. The tears of snakes remain under the watch-glass-like cutis with which the eyes are covered. The sclerotic often contains cartilage which may ossify. A vascular organ, the **processus falciformis**, passes from the middle of the choroid into the interior of the vitreous body in osseous fishes, its anterior extremity being termed the campanula Halleri. Similarly, there is the **pecten** in birds, but it is provided with muscular fibres. In birds the cornea is surrounded by a bony ring.

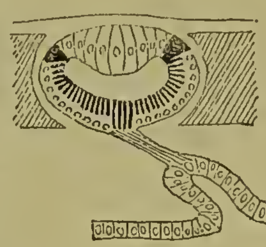


Fig. 710.
Section of the pineal eye of a lizard.

The whale has an enormously thick sclerotic. In **aquatic animals**, the lens is nearly spherical. The **muscles** of the **iris** and choroid are transversely striped in birds and reptiles. The retinal rods in all vertebrates are directed from before backwards, while the analogous elements (crystal rods and spheres) in invertebrata are directed from behind forward.

Historical.—The Hippocratic School were acquainted with the optic nerve and lens. Aristotle (384 B.C.) mentions that section of the optic nerve causes blindness—he was acquainted with after-images, short and long sight. Herophilus (307 B.C.) discovered the retina, and the ciliary processes received their name in his school. Galen (131–203 A.D.) described the six muscles of the eyeball, the puncta lachrymalia, and tear duct. Acrengar (1521) was aware of the fatty matter at the edge of the eyelids. Stephanus (1545) and Casseri (1609) described the Meibomian glands, which were afterwards redescribed by Meibom (1666). Fallopius described the vitreous membrane and the ciliary ligament. Plater (1583) mentions that the posterior surface of the lens is more curved. Aldrovandi observed the remainder of the pupillary membrane (1599). Observations were made at the time of Vesalius (1540) on the refractive action of the lens. Leonardo da Vinci compared the eye to a camera obscura. Maurolykos compared the action of the lens to that of a lens of glass, but it was Kepler (1611) who first showed the true refractive index of the lens and the formation of the retinal image, but he thought that during accommodation the retina moved forward and backward. The Jesuit, Scheiner († 1650), mentions, however, that the lens becomes more convex by the ciliary processes, and he assumed the existence of muscular fibres in the uvea. He referred long and short sight to the curvature of the lens, and he first showed the retinal image in an excised eye. With regard to the use of **spectacles** there is a reference in Pliny. It is said that at the beginning of the 14th century the Florentine, Salvino d'Armato degli Armati di Fir (†1317), and the monk, Alessandro de Spina (†1313), invented spectacles. Kepler (1611) and Descartes (1637) described their action. Mayo (†1852) described the 3rd nerve as the constrictor nerve of the pupil. Zinn contributed considerably to our knowledge of the structure of the eye. Ruysch described muscular fibres in the iris, and Monro described the sphincter of the pupil (1794). Jacob described the bacillary layer of the retina—Sœmmering (1791) the yellow spot. Brewster and Chossat (1819) tested the refractive indices of the optical media. Purkinje (1819) studied subjective vision.

Hearing.

406. THE ORGAN OF HEARING.—Stimulation of the Auditory Nerve.—The normal manner in which the auditory nerve is excited is by means of **sonorous vibrations**, which set in motion the end-organs of the acoustic nerve, lying in the endolymph of the labyrinth of the inner ear, on the membranous expansions of the cochlea and in the semicircular canals. Hence, the sonorous vibrations are first transmitted to the fluid in the labyrinth, and this, in turn, is thrown into waves, which set the end organs into vibration. Thus, the excitement of the auditory nerves is brought about by the *mechanical stimulation of the end-organs of the auditory nerve due to the wave-motion of the lymph of the labyrinth.*

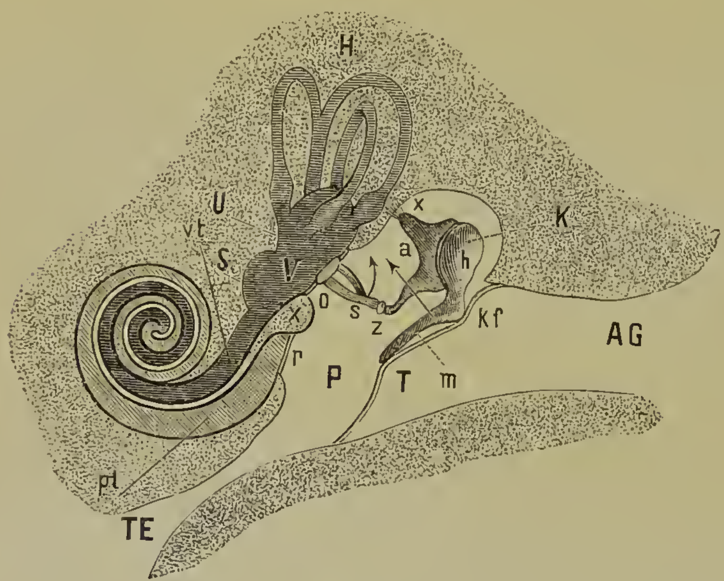


Fig. 711.

Scheme of the organ of hearing. AG, external auditory meatus ; T, tympanic membrane ; K, malleus with its head (*h*), short process (*kf*), and handle (*m*) ; *a*, incus, its short process (*x*), and its long process united to the stapes (*s*) by means of the Sylvian ossicle (*z*) ; P, middle ear ; *o*, fenestra ovalis ; *r*, fenestra rotunda ; *x*, beginning of the lamina spiralis of the cochlea ; *pt*, scala tympani, and *vt*, scala vestibuli ; V, vestibule ; S, saccule ; U, utricle ; H, semicircular canals ; TE, Eustachian tube. The long arrow indicates the line of traction of the tensor tympani ; the short curved one, that of the stapedius.

The fluid or lymph of the labyrinth is surrounded by the exceedingly hard osseous mass of the temporal bone (fig. 711). Only at one small roundish and slightly triangular area, the **fenestra rotunda** (*r*), the fluid is bounded by a delicate yielding membrane, which is in contact with the air in the middle ear or tympanum (P). Not far from the fenestra rotunda is the **fenestra ovalis** (*o*), in which the base of the stapes (*s*) is fixed by means of a yielding membranous ring. The outer surface of this also is in contact with the air in the middle ear. As the perilymph of the inner ear is in contact at these two places with a yielding boundary, it is clear that the lymph itself may exhibit oscillatory movements, as it must follow the movements of the yielding boundaries.

The sonorous vibrations may set the perilymph in vibration in *three* different ways:—

1. **Conduction through the Bones of the Head.**—This occurs especially when the vibrating solid body is applied directly to some part of the head, *e.g.*, a tuning-fork placed on the head, the sound being propagated most intensely in the direction of the prolongation of the handle of the instrument—also when the sound is conducted to the head by means of fluid, as when the head is ducked under water. Vibrations of the air, however, are practically not transferred directly to the bones of the head, as is shown by the fact that we are deaf when the ears are stopped.

The soft parts of the head, which lie immediately upon bone, conduct sound best, and of the projecting part, the best conductor is the cartilaginous portion of the external ear. But even under the most favourable circumstances, conduction through the bones of the head is far less effective than the conduction of the sound-waves through the external auditory meatus. If a tuning-fork be made to vibrate between the teeth until we no longer hear it, its tone may still be heard on bringing it near the ear (*Rinne*). The conduction through the bones is favoured when the oscillations are not transferred from the bones to the tympanic membrane, and are thus transferred to the air, in the outer ear. Hence, we hear the sound of a tuning-fork applied to the head better when the ears are stopped, as this prevents the propagation of the sound-waves through the air in the outer ear. If, in a *deaf* person the conduction is still normal through the cranial bones, then the cause of the deafness is not in the nervous part of the ear, but in the external sound-conducting part of the apparatus.

2. **Normal hearing** takes place through the **external auditory meatus.** The enormous vibrations of the air first set the tympanic membrane in vibration (fig. 711, T); this moves the malleus (h), whose long process is inserted into it; the malleus moves the incus (a), and this the stapes (s), which transfers the movements of its plate to the perilymph of the labyrinth.

3. **Direct Conduction to the Fenestra.**—In man, in consequence of occasional disease of the middle ear, whereby the tympanic membrane and auditory ossicles may be destroyed, the auditory apparatus may be excited, although only in a very feeble manner, by the vibrations of the air being directly transferred to the membrane of the fenestra rotunda (r), and the parts closing the fenestra ovalis (o). The membrane of the fenestra rotunda may vibrate alone, even when the oval window is closed with a rigid body (*Weber-Liel*).

407. PHYSICAL INTRODUCTION.—**Sound** is produced by the vibration of elastic bodies capable of vibration. Alternate **condensation** and **rarefaction** of the surrounding air are thus produced; or, in other words, **sound-waves** in which the particles vibrate longitudinally or in the direction of the propagation of the sound are excited. Around the point of origin of the sound, these condensations and rarefactions occur in equal concentric circles, which conduct the sound vibrations to our outer ear. The vibrations of the sounding body are so called "stationary vibrations," *i.e.*, all the particles of the vibrating body are always in the same phase of movement, in that they pass into movement simultaneously, they reach the maximum of movement simultaneously, *e.g.*, in the particles of a sounding vibrating metal rod. Sound is **produced** by the stationary vibrations of elastic bodies; it is **propagated** by progressive wave-motion of elastic media, generally the air. The wave-length of a tone, *i.e.*, the distance of one maximum of condensation to the next one in the air, is proportional to the duration of the vibration of the body, whose vibrations produce the sound-waves.

If γ is the wave-length of a tone, t in seconds the duration of a vibration of the body producing the wave, then $\gamma = n\ t$, where $n = 340{\cdot}88$ metres, which is the rate per second of propagation of sound-waves in the air. The rapidity of the transmission of sound-waves in water = 1435 metres per second, *i.e.*, nearly four times as rapid as in air; while, in solids capable of vibration, it is propagated from seven to eighteen times faster than in the air. Sound-waves are conducted best through the same medium; when they have to pass through several media they are always weakened.

Reflection of the sound-waves occurs when they impinge upon a solid obstacle, in which case the angle of reflection is always equal to the angle of incidence.

Wave Movements.—We distinguish—**I. Progressive wave movements** which occur in two forms—(1) As *longitudinal waves*, in which the individual particles of the vibrating body vibrate around their centre of gravity in the direction of the propagation of the wave; examples are the waves in water and air. This movement causes an accumulation of the particles at certain places, *e.g.*, on the crests of the waves in water-waves, while at other places they are diminished. This kind of wave is called a wave of **condensation** and **rarefaction**. (2) If, however, each particle in the progressive wave moves *vertically* up and down, *i.e.*, transversely to the direction of the propagation of the wave, then we have the simple *transverse waves*, or progressive waves, in which there is no condensation or rarefaction in the direction of propagation, as each particle is merely displaced laterally. An example of this is the *progressive waves in a rope.*

II. Stationary Flexion Waves.—When all the particles of an elastic vibrating body so oscillate that all of them are always in the same phase of movement as the limbs of a vibrating tuning-fork or a plucked string, then this kind of movement is described as stationary flexion waves. As bodies, whose expansion in the direction of oscillation is very slight, vibrate to and fro in the stationary flexion wave, so we see that the small parts of the auditory apparatus (tympanic membrane, ossicles, lymph of the labyrinth) oscillate in stationary flexion waves.

408. EAR MUSCLES—EXTERNAL AUDITORY MEATUS.—When the **external ear** is absent, little or no impairment of the hearing is observed; hence, the physiological functions of these organs are but slight. Boerhaave thought that the elevations and depressions of the outer ear might be connected with the reflection of the sound-waves. Numerous sound-waves, however, must be again reflected outwards; and those waves which reach the deep part of the concha are said to be reflected towards the tragus, to be reflected by it into the external auditory meatus. According to Schneider, when the depressions in the ear are filled up with wax, hearing is impaired; other observers, however, have found the hearing to be unaffected. Mach points out that the dimensions of the external ear are proportionally too small to act as reflecting organs for the wave-lengths of noises.

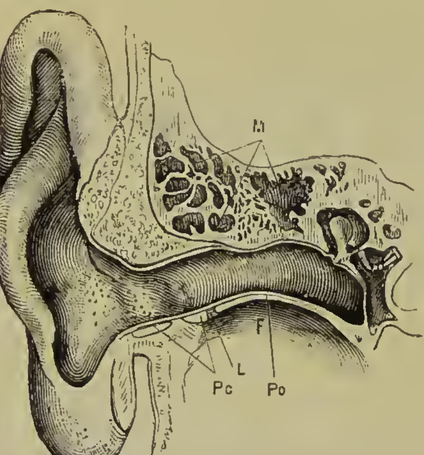


Fig. 712.

The auricle, external auditory meatus, and the tympanic cavity. M, osseous spaces in the temporal bone; Pc, cartilaginous part of the meatus; L, membranous union between both; F, auricular surface for the condyle of the lower jaw.

Muscles of the External Ear.—(1) The whole ear is moved by the retrahentes, attrahens, and attolens. (2) The *form* of the ear may be altered by the tragicus, antitragicus, helicis major and minor *internally;* and by the transversus and obliquus auriculæ *externally.* Persons who can move their ears do not find that the hearing is influenced during the movement. The Mm. helicis major and minor are regarded as elevators of the helix, the transversus and obliquus auriculæ as dilators of the concha; the tragicus and antitragicus as constrictors of the meatus. In animals, the external ear and the action of its muscles have a marked effect upon hearing. The muscles point the ear in the direction of the sound, while other muscles contract or dilate the space within the external ear. In many diving animals, the meatus can be closed by a kind of valve. The external auricle of man is a typically formed organ, but its function has been largely lost.

The **external meatus** is 3 to 3·25 cm. long [$1\frac{1}{8}$ to $1\frac{1}{4}$ inch], 8 to 9 mm. high, and 6 to 8 mm. broad at its outer opening (fig. 712). It is the conductor of the sound-waves to the tympanic membrane, so that almost all the sound-waves first impinge upon its wall, and are then reflected towards the tympanic membrane. To see well down into the meatus, we must pull the auricle upwards and backwards. Occlusion of the meatus, especially by a plug of inspissated wax (§ 287) of course interferes with the hearing, [and when it presses on the membrana tympani may give rise to severe vertigo].

409. TYMPANIC MEMBRANE.—The **tympanic membrane**, which is tolerably laxly fixed in a special osseous cleft, with a thickened margin, is an elastic, unyielding, and almost non-extensible membrane of about 0·1 mm. in thickness, and with a superficial area of 50 square millimetres (fig. 715). It is elliptical in form, its greater diameter being 9·5 to 10 mm. and its lesser 8 mm., and it is fixed in the floor of the external meatus obliquely, at an angle of 40°, being directed from above and outwards, downwards and inwards. Both tympanic membranes converge anteriorly, so that if both were prolonged they would meet to form an angle of 130° to 135°. The oblique position enables a larger surface to be presented than would be obtained if it were stretched vertically, so that more sound-waves can fall vertically upon it. The membrane is not stretched flat, but a little under its centre (umbilicus) it is drawn slightly inwards by the handle of the malleus, which is attached to it; while the short process of the malleus slightly bulges out the membrane near its upper margin (figs. 711, 718).

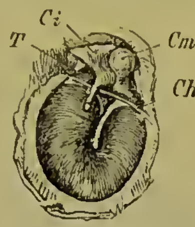


Fig. 713.

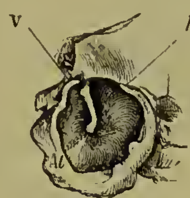


Fig. 715.

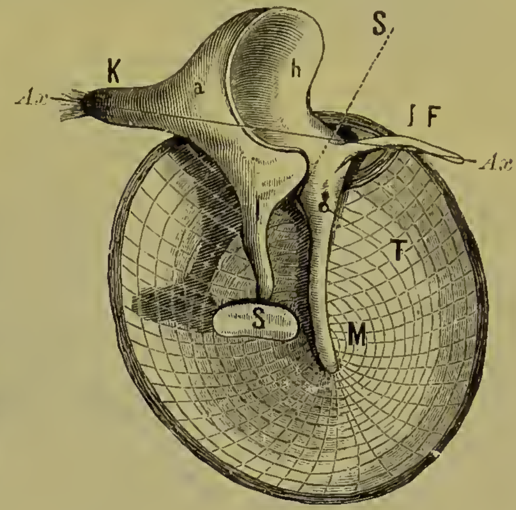


Fig. 714.

Fig. 713.—Tympanic membrane with the auditory ossicles (left) seen from within. *Ci*, incus; *Cm*, malleus; *Ch*, chorda tympani; *T*, pouch-like depression. Fig. 714.—Tympanic membrane and the auditory ossicles (left) seen from within, *i.e.*, from the tympanic cavity. M, manubrium or handle of the malleus; T, insertion of the tensor tympani; *h*, head; *lF*, long process of the malleus; *a*, incus, with the short (K) and the long (*l*) process; S, plate of the stapes; *Ax*, *Ax*, is the common axis of rotation of the auditory ossicles; S, the pinion-wheel arrangement between the malleus and incus. Fig. 715.—Tympanic membrane of a new-born child seen from without, with the handle of the malleus visible on it. *At*, tympanic ring with its anterior (*v*) and posterior (*h*) ends.

Structure.—The tympanic membrane consists of **three layers**:—(1) The **membrani propria** is a fibrous membrane with **radial** fibres on its outer surface, and **circularly** arranged fibres on its inner aspect. (2) The surface directed towards the meatus is covered with a thin and semi-transparent part of the **cutis**. (3) The side towards the tympanum is covered with a delicate mucous membrane, with simple **squamous epithelium.** Numerous nerves and lymph-vessels, as well as inner and outer blood-vessels, occur in the membrane.

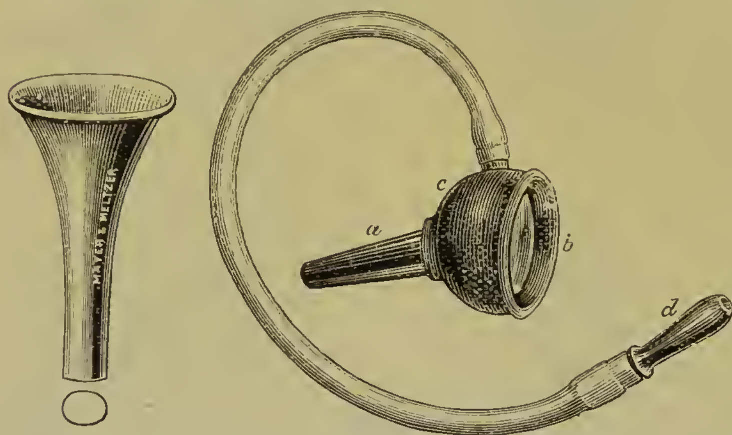
[The middle layer, or substantia propria, is fixed to a ring of bone, which is deficient above. This deficiency, however, is filled up by a layer composed of the mucous and cutaneous layers called the *membrana flaccida*, or Shrapnell's membrane.]

[**Examination of the tympanic membrane.**—When examining the outer ear and membrana tympani, pull the auricle upwards and backwards. The membrana tympani is examined by means of an **ear speculum** (fig. 716). The speculum is placed in the ear, and light is reflected into it by means of a concave mirror, perforated in the centre, and having a focal distance of four or five inches. It is convenient to have the mirror fixed to a band placed round the head as in the case of the laryngoscopic reflector (fig. 437). It is important to remember that the membrane is placed obliquely, so that the posterior and upper parts are nearer the surface. The membrane in health is greyish in colour and transparent, so that the handle of the malleus is seen running from above downwards and backwards, while at the anterior and inferior part there is a cone of light with its apex directed inwards.]

[**Siegle's Ear Speculum.**—"For further determining the presence of adhesions of the membrane and the mobility of the malleus, the pneumatic speculum first introduced by Siegle is very valuable. It consists (*vide* fig. 716) of an ordinary vulcanite speculum (*a*), which screws

into a vulcanite box (*c*) covered with a glass lens (*b*), which is also screwed on. By placing a little piece of india-rubber tubing on the tubular part, it fits air-tight into the meatus. The box has an india-rubber tube and a mouth-piece (*d*) connected with it, which is placed in the mouth of the surgeon ; suction is applied to the end of the tube, and the air drawn from the meatus, thus acting on the membrane, with a good light thrown on it through the speculum ; the former is seen magnified, and any adhesions and inequalities which may exist are disclosed."—*Macnaughton Jones.*]

Function of the tympanic membrane.—The tympanic membrane catches up the sound-waves which penetrate into the external meatus, and is set into vibration by them, the vibrations corresponding in number and amplitude to the vibrating movements of the air. Politzer connected the auditory ossicles fixed to the tympanic membrane of a duck with a recording apparatus, and could thus register the vibrations produced by sounding any particular tone. Owing to its small dimensions, the tympanic membrane can vibrate *in toto*, to and fro in the direction of the sound-waves corresponding to the condensations and rarefactions of the vibrating air, and therefore executes *transverse vibrations*, for which it is specially adapted, owing to the relatively slight resistance.



A B

Fig. 716.

Various forms of ear specula. A, ordinary form ; B, Siegle's ear pneumatic speculum.

Fundamental Note.—Stretched strings and membranes are generally only thrown into actual and considerable sympathetic vibration when they are affected by tones which correspond with their own fundamental tone, or whose number of vibrations is some multiple of the number of vibrations of the same, as the octave. When other tones act on them, they exhibit only inconsiderable sympathetic vibration. If a membrane be stretched over a funnel or cylinder, and if a nodule of sealing wax attached to a silk thread be made just to touch the centre of the membrane, then the sealing wax remains nearly at rest when tones or sounds are made in the neighbourhood ; as soon, however, as the fundamental or proper tone of this arrangement is sounded, the nodule is propelled by the strong vibrations of the membrane.

If we apply this to the tympanic membrane, then it also should exhibit very great vibrations when its own fundamental note is sounded, but only slight vibrations when other tones are produced. This, however, would produce great inequality in the audible sounds. There is an arrangement of the membrane whereby this is prevented. (1) Great resistance is offered to the vibrations of the tympanic membrane, owing to its union with the auditory ossicles. These act as a **damping apparatus**, which provides, as in damped membranes generally, that the tympanic membrane shall not exhibit excessive sympathetic vibrations for its own fundamental note. But the damping also makes the sympathetic vibrations less for all the other tones. In this way, *all* vibrations of the tympanic membrane are modified ; especially, however, is the excessive vibration diminished during the sounding of its fundamental tone. The membrane is at the same time rendered more capable of responding to the vibrations of different wave-lengths. The damp-

ing also *prevents after-vibrations.* (2) Corresponding to the small *mass* of the tympanic membrane, its sympathetic vibrations must also be small. Nevertheless, these slight elongations are quite sufficient to convey the sonorous movements to the most delicate end-organs of the auditory nerve; in fact, there are arrangements in the tympanum which still further diminish the vibrations of the tympanic membrane.

As v. Helmholtz has shown, the strong sympathetic vibrations of the tympanic membrane are not completely set aside by this damping arrangement. The painful sensations produced by some tones are, perhaps, due to the sympathetic vibration of the membrana tympani. According to Kessel, certain parts of the membrane vibrate to certain tones; the shortest radial fibres at the upper part of the anterior and upper segment vibrate with the highest tones, the longest fibres at the posterior segment with the deepest tones. At the upper part of the posterior segment noises are transmitted.

According to Fick, the tympanic membrane, besides possessing the property of taking up all vibrations with nearly equal intensity, has also the properties of a resonance apparatus; *i.e.*, it causes a summation of the energy of successive vibrations. This is due to the funnel shape of the membrane, and to the radial, rigid insertion of the handle of the malleus.

Fig. 717.
Toynbee's artificial membrana tympani.

Pathological.—Thickenings or inequalities of the tympanic membrane interfere with the acuteness of hearing, owing to the diminished capacity for vibration thereby produced. Holes in and loss of its substance act similarly. In extensive destruction, an artificial tympanum is placed in the external meatus, and its vibrations, to a certain extent, replace those of the lost membrane (*Toynbee*). [Fig. 717 shows an artificial tympanic membrane.]

410. AUDITORY OSSICLES AND THEIR MUSCLES.—The auditory ossicles have a **double function.**—(1) By means of the "chain" which they form, they transfer the vibrations of the tympanic membrane to the perilymph of the labyrinth. (2) They also afford points of attachment for the muscles of the middle ear, which can alter the *tension* of the membrana tympani, and the *pressure* on the lymph of the labyrinth.

Mechanism.—The *form* and *position* of the ossicles are given in figures 718 and 719. They form a jointed *chain* which connects the tympanic membrane, M, by means of the malleus, *h*, incus, *a*, and stapes, S, with the perilymph of the labyrinth. The **mode of movement** of the ossicles is of special importance. The handle of the malleus is firmly united to the fibres of the tympanic membrane (fig. 719, *n*). Besides this, the malleus is fixed by *ligaments* which prescribe the direction of its movements. Two ligaments—the lig. mallei anticum (passing from the processus Folianus) and the posticum (from a small crest on the neck)—together form a common axial band (*v. Helmholtz*), which acts in the direction from behind forwards, *i.e.*, parallel to the surface of the tympanic membrane. The neck of the malleus lies between the insertions of both ligaments. The united ligament determines the "**axis of rotation**" of the movement of the malleus.

When the handle of the malleus is drawn *inwards*, of course its head moves in the opposite direction, or outwards. The *incus*, *a*, is only partially fixed by a ligament, which attaches its short process to the wall of the tympanic cavity, in front of the entrance to the mastoid cells, *k*. The not very tense articulation joining it to the head of the malleus, *h*, which lies with its saddle-shaped articular surface in the hollow of the incus, is important. The lower margin of the incus (fig. 719, S) acts like a tooth of a cog-wheel. Thus, when the handle of the malleus moves inwards to a tympanic cavity, the incus, and its long process, *b*, which is parallel to the handle of the malleus, also pass inwards. The incus forms almost a right angle with the stapes, S, through the intervention of the Sylvian ossicle, *s*. If, however, as by condensation of the air in the tympanum, the membrana tympani and the handle of the malleus move *outwards*, the long process of the incus does not make a similar movement, as the malleus moves away

from this margin of the incus. Hence the stapes is not liable to be torn from its socket. The malleus and incus form an **angular lever**, which moves round a common axis (fig. 718 and fig. 719, *Ax*, *Ax*). In the *inward* movement, the malleus follows the incus, as if both formed one piece. The *common axis* (fig. 714) is not, however, the axial ligament of the malleus, but it is formed *anteriorly* by the processus Folianus, *lF*, directed forwards, and *posteriorly* by the short process of the incus directed backwards. The rotation of both ossicles around this axis occurs in a plane vertical to the plane of the membrana tympani. During the rotation, of course the parts above this axis (head of the malleus and upper part of the body of the incus) take a direction opposite to the parts lying below it (the handle of the malleus and the long process of the incus), as is indicated in fig. 719 by the direction of the arrows. The

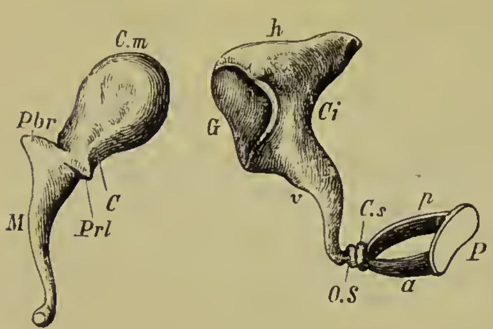


Fig. 718.

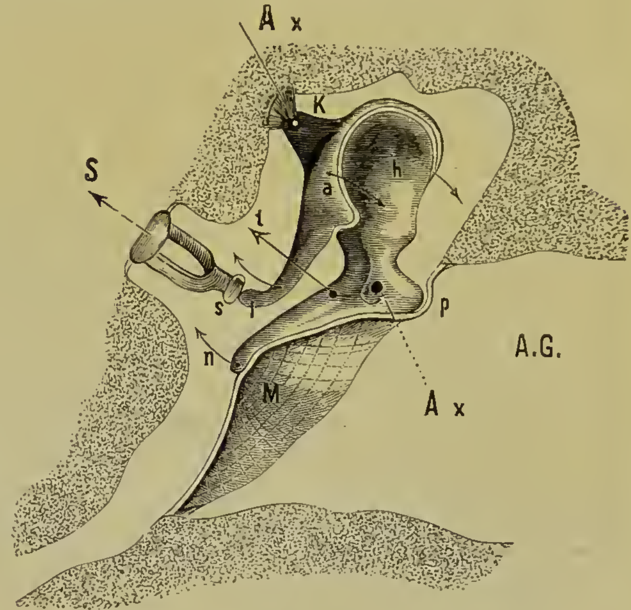


Fig. 719.

Fig. 718.—The auditory ossicles (right). *C.m*, head ; *C*, neck ; *Pbr*, short process ; *Prl*, long process ; *M*, handle of the malleus ; *Ci*, body ; *G*, articular surface ; *h*, short, and *v*, long process of the incus ; *O.S*, so-called lenticular ossicle ; *C.s*, head ; *a*, anterior, and *p*, posterior limb, *P*, plate of the stapes. Fig. 719.—Tympanum and auditory ossicles (left) magnified. A.G., external meatus ; M, membrana tympani, which is attached to the handle of the malleus, *n*, and near it the short process, *p* ; *h*, head of the malleus ; *a*, incus ; *k*, its short process with its ligament ; *l*, long process ; *s*, Sylvian ossicle ; S, stapes ; *x*, *Ax*,*A* is the axis of rotation of the ossicles ; it is shown in perspective, and must be imagined to penetrate the plane of the paper ; *t*, line of traction of the tensor tympani. The other arrows indicate the movement of the ossicles when the tensor contracts.

movement of the handle of the malleus must follow that of the membrana tympani, and *vice versâ*, while the movement of the stapes is connected with the movement of the long process of the incus. As the long process of the incus is only two-thirds of the length of the handle of the malleus (figs. 711, 715, 719), of course the *excursion* of the tip of the former, and with it of the stapes, must be correspondingly *less* than the movement of the tip of the handle of the malleus, while, on the other hand, the *force* of the movement of the tip of the handle of the malleus, corresponding to the diminution of the excursion, will be *increased*.

Mode of Vibration.—Thus, the movement of the membrana tympani inwards causes a less extensive but a *more powerful* movement of the foot of the stapes against the perilymph of the labyrinth. V. Helmholtz and Politzer calculated the extent of the movement to be 0·07 mm. The mode in which the vibrations of the membrana tympani are conveyed to the lymph of the labyrinth, through the chain of ossicles, is quite analogons to the mechanism of these parts already described. Long delicate glass threads were fixed to these ossicles, and their movements

were thus graphically recorded on a smoked surface (*Politzer*, *Hensen*). Or, strongly refractive particles were so fixed to the ossicles that the beam of light reflected from them could be examined by means of a microscope (*Buck*, *v. Helmholtz*). All the experiments showed that the transference of the sound-waves is accomplished by means of the mechanism of the **angular lever**, composed of the auditory ossicles already described. As the vibrations of the membrana tympani are conveyed to the handle of the malleus, they are weakened to about one-fourth of their original strength (*Politzer*). [The membrana tympani is many times (30) larger than the fenestra ovalis, and the relation in size might be represented by a funnel. The arm of the malleal end of the lever where the power acts is 9½ mm. long, while the short or stapedial arm is 6½ mm., so that the latter moves less than the former, but what is lost in extent is gained in force.]

[**Methods.**—Politzer attached small, very light levers to each of the ossicles, and inscribed their movements on a revolving cylinder. An organ-pipe was sounded, and when the levers were of the same length, the malleus made the greatest excursion and the stapes the least. Buck attached starch grains to the ossicles, illuminated them, and observed the movements of the refractive starch granules by means of a microscope provided with a micrometer.]

The **ossicles** move *en masse*, and not in the way of propagating molecular vibrations. As the excursions of the ossicles during sonorous vibrations are, however, only nominal, there is practically no change in the position of the joints with each vibration. The latter will only occur when extensive movements take place by means of the muscles.

The **muscles** of the auditory ossicles alter the position and tension of the membrana tympani, as well as the pressure of the lymph of the labyrinth. The **tensor tympani**, which lies in an osseous groove above the Eustachian tube, has its tendon deflected round an osseous projection [processus cochleariformis], which lies external to it, almost at right angles to the groove above it, and is inserted immediately above the axis of rotation of the malleus (fig. 714, M). When the muscle contracts in the direction of the arrow, *t*, then the handle of the malleus (*n*) pulls the membrana tympani (M) inwards and tightens it (fig. 719). This also causes a movement of the incus and stapes (S) which must be pressed more deeply into the fenestra ovalis as already described. When the muscle relaxes, then owing to the *elasticity* of the rotated axial ligament and the tense membrana tympani itself, the position of equilibrium is again restored. The **motor nerve** of this muscle arises from the trigeminus, and passes through the *otic ganglion* (§ 347, III. 6). C. Ludwig and Politzer observed that stimulation of the fifth nerve within the cranium [dog] caused the above-mentioned movement.

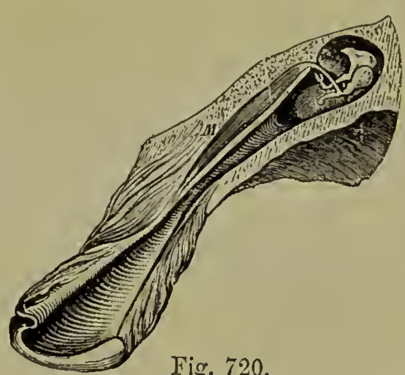


Fig. 720.
Tensor tympani—the Eustachian tube (left).

Use of the tension.—The tension of the membrana tympani caused by the tensor tympani has a double function (*Joh. Müller*)—**1.** The tense membrane offers very great resistance to sympathetic vibrations when the sound-waves are very intense, as it is a physical fact that stretched membranes are more difficult to throw into sympathetic vibrations the tenser they are. Thus, the tension so far protects the auditory organ, as it prevents too intense vibrations affecting the membrana tympani from reaching the terminations of the nerves. **2.** The tension of the membrana tympani must vary according to the degree of contraction of the tensor. Thus, the membrana for the time being has a different fundamental tone, and is thereby capable of vibrating to the correspondingly higher tone, it, as it were, being in a certain sense accommodated for.

Comparison with Iris.—The membrana tympani has been compared with the iris. Both membranes prevent, by contraction—narrowing of the pupil and tension of the membrana tympani—the too intense action of the specific stimulus from causing too great stimulation, and both *adapt* the sensory apparatus, for the action of moderate or weak stimuli. This movement in both membranes is brought about *reflexly*, in the ear through the N. acusticus, which causes a reflex stimulation of the motor fibres for the tensor tympani.

Effect of Tension.—That increased tension of the membrana tympani renders it less sensitive to sound-waves is easily proved thus:—Close the mouth and nose, and make either a forced expiration, so that the air is forced into the Eustachian tube, which bulges out the membrana tympani, or inspire forcibly, whereby the air in the tympanum is diminished, so that the membrana bulges inwards. In both cases, hearing is interfered with, as long as the increased tension lasts. If a funnel with a small lateral opening, and whose wide end is covered by a membrane, be placed in the external meatus, hearing becomes less distinct when the membrane is stretched (*Joh. Müller*). If air be blown into the external auditory meatus, both tensores tympani contract, and in consequence of this the hearing of the other ear is temporarily affected (*Gellé*).

Normally, the tensor tympani is excited *reflexly*. The muscle is not directly and by itself subject to the control of the will. According to L. Fick, the following phenomenon is due to an "associated movement" of the tensor:—When he pressed his jaws firmly against each other, he heard in his ear a piping, singing tone, while a capillary tube, which was fixed air-tight into the meatus, had a drop of water which was in it rapidly drawn inwards. During this experiment, a person with normal hearing hears all musical tones as if they were louder, while all the highest non-musical tones are enfeebled (*Lucae*). When *yawning*, v. Helmholtz and Politzer found that hearing was enfeebled for certain tones.

Contraction of the Tensor.—Hensen showed that the contraction of the tensor tympani during hearing is not a continued contraction, but what might be termed a "twitch." A twitch takes place at the beginning of the act of hearing, which favours the perception of the sound, as the membrana tympani thus set in motion vibrates more readily to higher tones than when it is at rest. On exposing the tympanum in cats and dogs, it was found that this contraction or twitch occurs only at the beginning of the sound, and that it soon ceases, although the sound may continue.

Action of the Stapedius.—The muscle arises within the eminentia pyramidalis, and is inserted into the head of the stapes and Sylvian ossicle (fig. 721); when it draws upon the head of the stapes, as indicated in fig. 711, by the small curved arrow, it must place the bone obliquely, whereby the posterior end of the plate of the stapes is pressed somewhat deeper *inwards* into the fenestra ovalis, while the anterior is, as it were, displaced somewhat *outwards*. The stapes is thereby more fixed, as the fibrous mass [angular ligament] which surrounds the fenestra ovalis and keeps the stapes in its place becomes more tense. The activity of this muscle, therefore, prevents too intense shocks, which may be communicated from the incus to the stapes, from being conveyed to the perilymph. It is supplied by the **facial nerve** (§ 349, 3).

Fig. 721.
Right stapedius muscle.

The stapedius in many persons executes an *associated* movement, when the eyelids are forcibly closed (§ 349). Some persons can cause it to contract *reflexly* by scratching the skin in front of the meatus, or by gently stroking the outer margin of the orbit (*Henle*). It seems to be excited reflexly in many diseases of the ear when the tympanum is being syringed.

Other Views.—According to Lucae, when the stapes is displaced obliquely, its head forces the long process of the incus, and also the membrana tympani, *outwards*, so that it is regarded as an *antagonist* of the tensor tympani. Politzer observed that the pressure within the labyrinth fell when he stimulated the muscle. According to Toynbee, the stapedius acts as a lever and moves the stapes slightly out of the fenestra ovalis, thus making it more free to move, so that it is more capable of vibrating. Henle supposes that the stapedius is more concerned in *fixing* than in moving the stapes, and that it comes into action when there is danger of too great movement being communicated to the stapes from the incus. Landois agrees with this opinion, and compares the stapedius with the orbicularis palpebrarum, both being protective muscles.

Pathological.—Immobility of the auditory ossicles, either by adhesions or anchyloses, causing diminished vibrations, interferes with hearing; while the same result occurs when the stapes is firmly anchylosed into the fenestra ovalis. The tendon of the tensor tympani has been divided

in cases of contracture of the muscles. For paralysis of the tensor, see § 347, and for the stapedius, § 349.

411. **EUSTACHIAN TUBE—TYMPANUM.**—The **Eustachian tube** [4 centimetres in length ($1\frac{1}{4}$ in.), 2–3 mm. in width (fig. 722)] is the **ventilating tube** of the tympanic cavity. It keeps the tension of the air within the tympanum the same as that within the pharynx and outer air (figs. 711, 720). Only when the tension of the air is the same outside and inside the tympanum, is the normal vibration of the membrana tympani possible. The tube is generally *closed*, as the surfaces of the mucous membrane lining it come into apposition. During **swallowing**, however, the tube is opened, owing to the traction of the fibres of the tensor veli palatini [spheno-salpingo-staphylinus sive abductor tubae (*v. Tröltsch*), sive dilator tubae (*Rüdinger*)] inserted into the membrano-cartilaginous part of the tube (*Toynbee, Politzer*). (Compare § 139, 2.) When the tube is closed, the vibrations of the membrana tympani are transferred in a more undiminished condition to the auditory ossicles than when it is open, whereby part of the vibrating air is forced through the tube (*Mach and Kessel*). If, however, the tympanic cavity is closed *permanently*, the air within it becomes so rarefied (§ 139) that the membrana tympani, owing to the abnormally low tension, becomes drawn inwards, thus causing difficulty of hearing. As the tube is lined by ciliated epithelium it carries outwards to the pharynx the secretions of the tympanum (§ 291).

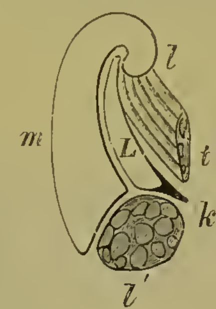


Fig. 722.
Schematic section of the Eustachian tube. *m* and *l*, lateral median plate; K, edge of the tube; *l'*, levator, and *t*, tensor palate; L, lumen of tube.

[**Functions of the Eustachian Tube.**—It permits the air in the tympanum to be changed, it acts as an outlet for secretions, maintains the equilibrium between the air in the tympanum and that in the external auditory meatus, and it prevents the rarefaction of the air in the tympanum produced by successive acts of swallowing.]

Noise in the Tube.—A sharp hissing noise is heard in the tube during swallowing, when we swallow slowly and at the same time contract the tensor tympani, due to the separation of the adhesive surfaces of its lining membrane. Another person may hear this noise by using a stethoscope or his ear.

In **Valsalva's experiment** (§ 60), as soon as the pressure of the air reaches 10 to 40 mm. Hg, air enters the tube. The sound is heard first, and then we feel the increased tension of the tympanic membrane, owing to the entrance of air into the tympanum. During forced inspiration, when the nose and mouth are closed, air is sucked out, while the tympanum is ultimately drawn inwards.

The M. levator veli palatini, as it passes under the base of the opening of the tube into the pharynx, forms the *levator-eminence* or cushion (fig. 432, W). Hence, when this muscle contracts and its belly thickens, as at the commencement of the act of deglutition and during phonation, the lower wall of the pharyngeal opening is raised, and the opening thereby narrowed (*Lucae*). The *contraction* of the tensor, occurring during the later part of the act of deglutition, dilates the tube.

Other views.—According to Rüdinger, the tube is always open, although only by a very narrow passage in the upper part of the canal, while the canal is dilated during swallowing. According to Cleland, the tube is generally open, and is closed during swallowing.

[**Practical Importance.**—The tympanic cavity forms an osseous box, and therefore a protective organ for the auditory ossicles and their muscles, while the increased air space, obtained by its communication with the mastoid cells, permits free vibration of the membrana tympani. The six sides of the tympanum have important practical relations. It is about half an inch in height, and one or two lines in breadth, *i.e.*, from without inwards. Its *roof* is separated from the cavity of the brain by a very thin piece of bone, which is sometimes defective, so that

encephalitis may follow an abscess of the middle ear. The *outer* wall is formed by the membrana tympani, while on the *inner* wall are the fenestra ovalis and rotunda, the ridge of the aqueductus Fallopii, the promontory, and the pyramid. The *floor* consists of a thin plate of bone, which roofs in the jugular fossa and separates it from the jugular vein. Fractures of the base of the skull may rupture the carotid artery or internal jugular vein; hence, hæmorrhage from the ears is a bad symptom in these cases. Caries of the ear may extend to other organs. The *anterior* wall is in close relation with the carotid artery, while the *posterior* communicates with the mastoid cells, so that fluids from the middle ear sometimes escape through the mastoid cells.]

That the air in the tympanum can communicate its vibrations to the membrane of the fenestra

Fig. 723.

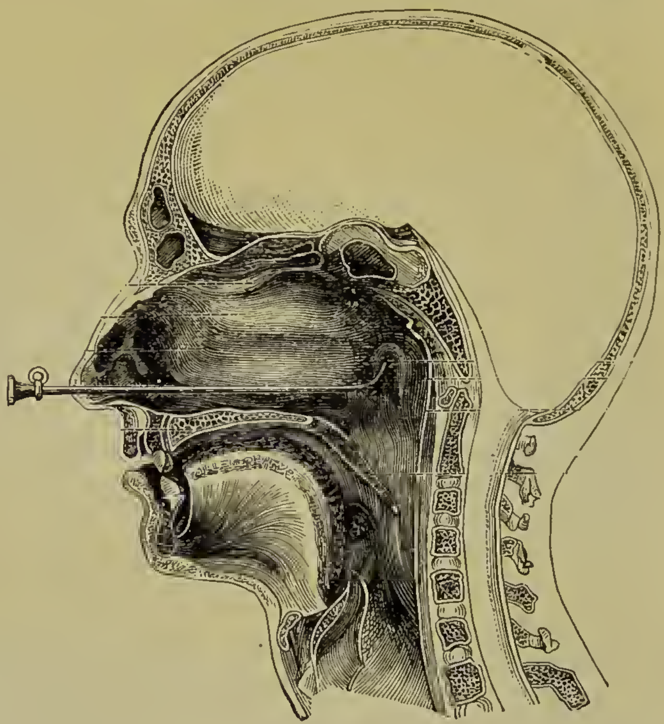


Fig. 724.

Fig. 723.—Bellows attached to an Eustachian catheter (*Macnaughton Jones*). Fig. 724.—Vertical section of the head, showing the Eustachian catheter in position.

rotunda is true (p. 976, 3), but *normally* this is so slight, when compared with the conduction through the auditory ossicles, that it scarcely need be taken into account.

Structure.—The tube and tympanum are lined by a common mucous membrane, covered by ciliated epithelium, while the membrana is lined by a layer of squamous epithelium. Mucous glands were found by Tröltsch and Wendt in the mucous membrane. [The epithelium covering the ossicles and tensor tympani is not ciliated.]

Pathological.—The tube is often occluded, owing to chronic catarrh and narrowing from cicatrices, hypertrophy of the mucous membrane, or the presence of tumours. The deafness thereby produced may often be cured by *catheterising* the tube from the nose (fig. 724). Effusions into or suppuration within the tympanum of course paralyse the sound-conducting mechanism, while inflammation often causes subsequent affections of the plexus tympaniens. If the temporal bone be destroyed by progressive caries within the tympanum, inflammation of the neighbouring cerebral structures may occur and cause death.

[**Methods.**—Not unfrequently the aurist is called upon to dilate the Eustachian tube, which in certain cases requires the use of a **Eustachian catheter** introduced into the tube along the floor of the nose (fig. 724). At other times he requires to fill the tympanic cavity with air, which is easily done by means of a **Politzer's bag** or inflating bellows (fig. 723). The nozzle is introduced into one nostril, while the other nostril is closed, and the patient is directed to

swallow, while at the same moment the surgeon compresses the bag, and the patient's mouth being closed, air is forced through the open Eustachian tube into the middle ear.]

[Politzer's ear-manometer (fig. 725) consists of a U-shaped small glass tube fixed in an india-rubber cork, so that the latter can be hermetically fixed in the meatus. A drop of coloured fluid is placed in the tube. During the first part of the act of swallowing—the nostrils and mouth being closed—the fluid rises slightly, but in the second part of the act it falls decidedly, owing to the rarefaction of the air in the tympanum.]

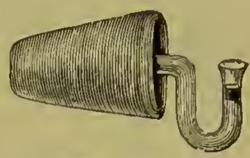


Fig. 725.
Politzer's ear-manometer.

412. CONDUCTION OF SOUND IN THE LABYRINTH.—The vibrations of the foot of the stapes in the fenestra ovalis give rise to waves in the perilymph within the inner ear or labyrinth. These waves are so-called "*flexion-waves*," *i.e.*, the perilymph moves in mass before the impulse of the base of the stapes. This is only possible from the existence of a *yielding* membrane—that filling the fenestra rotunda, and sometimes called the *membrana secundari*, which during rest bulges inwards to the scala tympani, and can be bulged outwards towards the tympanic cavity by the impulse communicated to it by the movement of the perilymph (fig. 711, *r*). The flexion waves must correspond in number and intensity to the vibrations of the auditory ossicles, and must also excite the free terminations of the auditory nerve, which float free in the endolymph.

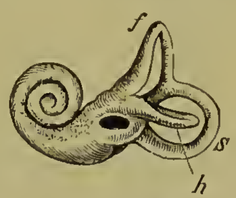


Fig. 726.
External appearance of the osseous labyrinth, fenestra ovalis, cochlea to the left, and (*f*) the upper, (*h*) horizontal, and (*s*) posterior semicircular canal (left).

As the endolymph of the saccule and utricle lying in the vestibule receives the first impulse, and as these communicate anteriorly with the cochlea, and posteriorly with the semicircular canals, consequently the motion of the perilymph must be propagated through these canals. To **reach the cochlea**, the movement passes from the *saccule* (lying in the fovea hemispherica) along the scala vestibuli to the helicotrema, where it passes into the scala tympani, where it reaches the membrane of the fenestra rotunda, and causes it to bulge outwards. From the *utricle* (lying in the fovea hemielliptica), in a similar manner the movement is propagated through the *semicircular canals.* Politzer observed that the endolymph in the superior semicircular canal rose when he caused contraction of the tensor tympani by stimulating the trigeminus, just as the base of the stapes must be forced against the perilymph with every vibration of the membrana tympani.

[**Practical.**—It is well to view the organ of hearing as consisting of two mechanisms :—

1. The sound-conducting apparatus.
2. The sound-perceiving apparatus.

The **former** includes the *outer* ear, with its auricle and external meatus ; the *middle* ear and the parts which bound it, or open into it. The **latter** consists of the *inner* ear with the expansion of the auditory nerve in the labyrinth, the nerve itself, and the sound-perceiving and interpreting centre or centres in the brain (§ 376, 2).]

[**Testing the Sound-conduction.**—In any case of deafness, it is essential to estimate the degree of deafness by the methods stated at § 406, and it is well to do so both for such sounds as those of a watch and conversation. We have next to determine whether the *sound-conducting* or the *sound-perceiving* apparatus is affected. If a person is deaf to sounds transmitted through the air, on applying a sounding tuning-fork (fig. 727), to the middle line of the head or teeth, if it be heard distinctly, then the sound-perceiving apparatus is intact, and we have to look for the cause of deafness in the outer or middle ear. In a healthy person,

the sound of the tuning-fork is heard of equal intensity in both ears. In this case the sound is conducted directly to the labyrinth by the cranial bones. In cases of disease of the sound-conducting mechanism, the sound of the tuning-fork is heard loudest in the *deafer* ear. Ed. Weber pointed out that, if one ear be stopped and a vibrating tuning-fork placed on the head, the sound is referred to the plugged ear, where it is heard loudest. It is assumed that when the ear is plugged, the sound-waves transmitted by the cranial bones are prevented from escaping (*Mach*). If, on the contrary, the sound be heard loudest in the good ear, then in all probability there is some affection of the sound-perceiving apparatus or labyrinth, although there are exceptions to this statement, especially in elderly people. Another plan is to connect two telephones with an induction machine, provided with a vibrating Neef's hammer. The sounds of the vibrations of the latter are reproduced in the telephones, and if they be placed to the ears, then the healthy ears hear only *one* sound, which is referred to the middle line, and usually to the back of the head. In diseased conditions this is altered—it is referred to one side or the other.]

Fig. 727. Aural tuning-fork.

413. LABYRINTH AND AUDITORY NERVE.—Scheme.—The **vestibule** (fig. 728, III) contains two separate sacs; one of them, the **saccule**, *s* (round sac or S. hemisphæricus), communicates with the **ductus cochlearis**, *Cc* of the cochlea; the other, the **utricle**, U (elliptical sac, or sacculus hemiellipticus), communicates with the semicircular canals, *Cs*, *Cs*.

The **cochlea** consists of $2\frac{1}{2}$ turns of a tube disposed round a central column or **modiolus**. The tube is divided into two compartments by a horizontal septum, partly osseous and partly membranous, the **lamina spiralis ossea** and **membranacea** (fig. 732, fig. 728, I). The **lower compartment** is the **scala tympani** and is separated from the cavity of the tympanum by the membrane of the fenestra rotunda.

The **upper compartment** is the **scala vestibuli**, which communicates with the vestibule of the labyrinth (fig. 728, I). These two compartments communicate directly by a small opening at the apex of the cochlea, a sickle-shaped edge ["hamulus"] of the lamina spiralis bounding the **helicotrema** (fig. 711). The scala vestibuli is divided by **Reissner's membrane** (fig. 728, I), which arises near the outer part of the lamina spiralis ossea, and runs obliquely outwards to the wall of the cochlea so as to cut off a small triangular canal, the **ductus** or **canalis cochlearis**, or **scala media**, *Cc*, whose floor is formed for the most part by the lamina spiralis membranacea, and on which the end-organ of the auditory nerve—**Corti's organ**—is placed. The lower end of the canalis cochlearis is blind, III, and divided towards the saccule, with which it communicates by means of the small **canalis reuniens**, *Cr* (*Hensen*). The **utricle** (fig. 728, III, U) communicates with the three semicircular canals *Cs*, *Cs*—each by means of an ampulla, within which lie the terminations of the ampullary nerves, but as the posterior and the superior canals unite, there is only one common ampulla for them. The membranous semicircular canals lie within the osseous canals, perilymph lying between the two. **Perilymph** also fills the scala vestibuli and s. tympani, so that all the spaces within the labyrinth are filled by fluid, while the spaces themselves are lined by short cylindrical epithelium.

The system of spaces, filled by **endolymph**, is the only part containing the nervous end-organs for hearing. All these spaces communicate with each other; the semicircular canals directly with the utricle, the ductus cochlearis with the

saccule through the canalis reuniens; and lastly, the saccule and utricle through the "**saccus endolymphaticus,**" which springs by an isolated limb from each sac; the limbs then unite as in the letter Y, and pass through the osseous aqueductus

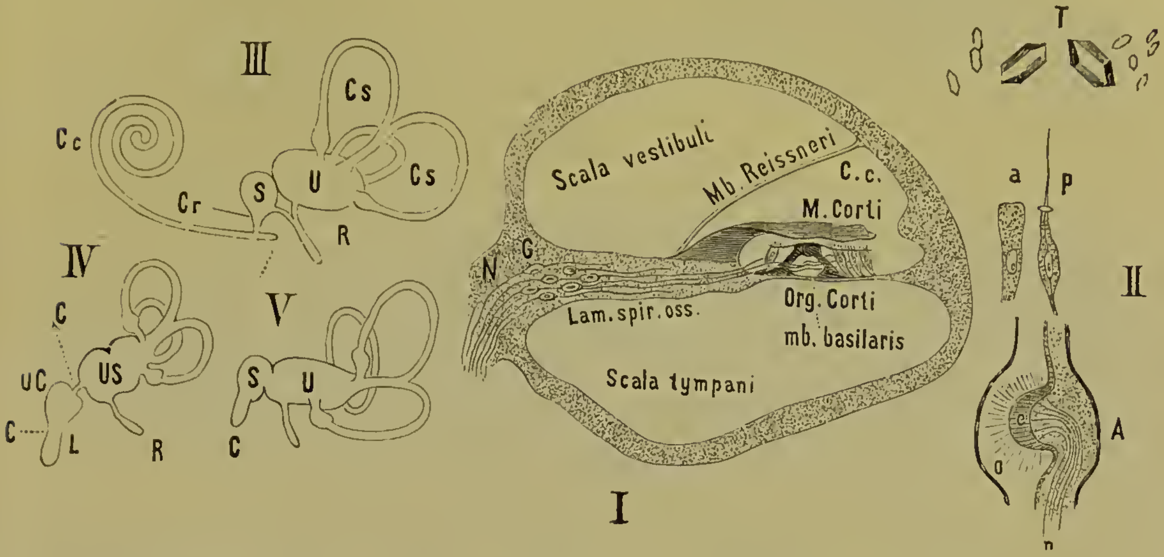


Fig. 728.

I, transverse section of a turn of the cochlea; II, A, ampulla of a semicircular canal with the crista acustica; *a*, *p*, auditory cells; *p*, provided with a fine hair; T, otoliths; III, scheme of the human labyrinth; IV, scheme of a bird's labyrinth; V, scheme of a fish's labyrinth.

vestibuli to end blindly in the dura mater of the brain (fig. 728 III, R). The aqueductus cochlea is another narrow passage, which begins in the scala tympani,

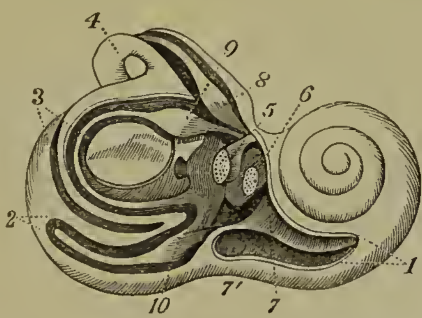


Fig. 729.

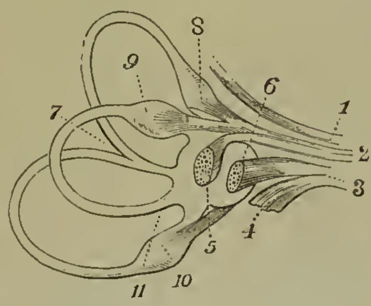


Fig. 730.

The interior of the right labyrinth with its membranous canals and nerves. In fig. 729 the outer wall of the bony labyrinth is removed to show the membranous parts within—1, commencement of the spiral tube of the cochlea; 2, posterior semicircular canal, partly opened; 3, horizontal; 4, superior canal; 5, utricle; 6, saccule; 7, lamina spiralis; 7′, scala tympani; 8, ampulla of the superior membranous canal; 9, of the horizontal; 10, of the posterior canal. Fig. 730 shows the membranous labyrinth and nerves detached—1, facial nerve in the internal auditory meatus; 2, anterior division of the auditory nerve giving branches to 5, 8, and 9, the utricle and the ampullæ of the superior and horizontal canals; 3, posterior division of the auditory nerve, giving branches to the saccule, 6, and posterior ampulla, 10, and cochlea, 4; 7, united part of the posterior and superior canals; 11, posterior extremity of the horizontal canal.

immediately in front of the fenestra rotunda, and opens close to the fossa jugularis. It forms a direct means of communication between the perilymph of the cochlea and the subarachnoid space.

Semicircular Canals and Vestibular Sacs.—The membranous semicircular canals do not fill the corresponding osseous canals completely, but are separated from them by a pretty wide space, which is filled with perilymph (fig. 729). At the concave margin they are fixed by connective-tissue to the osseous walls. The ampullæ, however, completely fill the corresponding osseous dilatations. The canals and ampullæ consist externally of an outer, vascular, connective-tissue layer, on which there rests a well-marked hyaline layer, bearing a single layer of flattened epithelium.

Crista Acustica.—The vestibular branch of the auditory nerve sends a branch to each ampulla and to the saccule and utricle (fig. 730). In the **ampullæ** (fig. 728, II, A), the nerve (*c*) terminates in connection with the **crista acustica**, which is a yellow elevation projecting into the equator of the ampulla. The medullated nerve-fibres, *n*, form a plexus in the connective-tissue layer, lose their myelin as they pass to the hyaline basement membrane, and each ends in a cell provided with a rigid hair (*o*, *p*), 90 μ in length, so that the crista is largely covered with these **hair-cells**, but between them are **supporting cells** like cylindrical epithelium (*a*), and not unfrequently containing granules of yellow pigment. The hairs or "**auditory hairs**" (*M. Schultze*) are composed of many fine fibres (*Retzius*). An excessively fine membrane (**membrana tectoria**) covers the hairs (*Pritchard*, *Lang*).

Maculæ Acusticæ.—The nerve-terminations in the maculæ acusticæ of the **saccule** and **utricle** are exactly the same as in the ampullæ, only the free surface of their membrana tectoria is sprinkled with small white chalk-like crystals or **otoliths** (fig. 728, II, T), composed of calcic carbonate, which are sometimes amorphous and partly in the form of arragonite, lying fixed in the viscid endolymph. The non-medullated axis-cylinders of the saccular nerves enter directly into the substance of the hair-cells. The terminations of the nerves have been investigated, chiefly in fishes, in the rays.

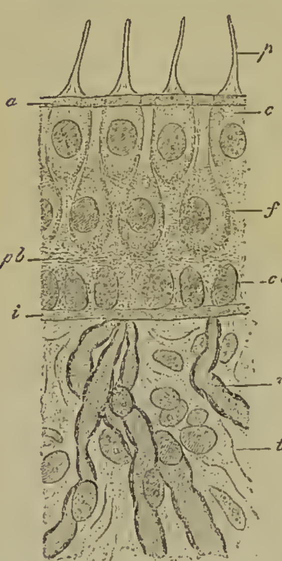


Fig. 731.

Vertical section of the macula acustica of rabbit.

[Fig. 731 is a vertical section of a macula acustica of the rabbit. The medullated nerves (*n*) lose their myelin at the external limiting membrane, become non-medullated, pierce this membrane, and form a basal plexus (*pb*) between (*i*) the epithelial cells, and finally terminate in the sensory ciliated cells (*p*). The epithelium itself consists of basal cells (*cb*), fusiform or supporting cells (*f*), and the ciliated neuro-epithelium (*p*), each cell being provided with a cilium, which perforates the external limiting membrane (*a*). There is thus a remarkable likeness to the olfactory epithelium.]

Cochlea.—The terminations of the cochlear branch of the auditory nerve lie in connection with **Corti's organ**, which is placed in the canalis or ductus cochlearis (fig. 728, I, *Cc*, and III, *Cc*, and fig. 732), the small triangular chamber [or scala media], cut off from the scala vestibuli by the membrane of Reissner. Corti's organ is placed on the lamina spiralis membranacea, and consists of a *supporting apparatus* composed of the so-called **Corti's arches**, each of which consist of two **Corti's rods** (*z y*), which lie upon each other like the beams of a house. But every two rods do not form an arch, as there are always three inner to two outer rods (*Claudius*). There are about 4500 outer rods (*Waldeyer*).

The ductus cochlearis becomes larger towards the apex of the cochlea, and the rods also become longer; the **inner** ones are 30 μ long in the first turn, and 34 μ in the upper, the **outer** rods 47 μ and 69 μ respectively. The span of the arches

also increases (*Hensen*). [The arches leave a triangular tunnel beneath them.] The proper end-organs of the cochlear nerve are the cylindrical "**hair-cells**" (*Kölliker*) previously observed by Corti, which are from 16,400 to 20,000 in number (*Hensen*, *Waldeyer*). There is *one* row of **inner cells** (*i*), which rests on a layer of small granular cells (K) (*Böttcher*, *Waldeyer*); the **outer cells** (*a*, *a*) number 12,000 in man (*Retzius*), and rest upon the basement membrane, being disposed in three or even four rows. Between the outer hair-cells there are other cellular structures, which are either regarded as special cells (**Deiter's cells**), or are regarded merely as processes of the hair-cells (*Lavdowsky*). [The cochlear branch of the auditory nerve enters the modiolus, and runs upwards in the osseous channels there provided for it, and as it does so gives branches to the lamina spiralis, where they run between the osseous plates which form the lamina.] The fibres (N) come out of the lamina spiralis after traversing the **ganglionic cells** in their course (figs. 728, 732, I, G), and end by fine varicose fibrils in the hair-cells (fig. 732) (*Waldeyer*, *Gottstein*, *Lavdowsky*, *Retzius*).

Membrana Reticularis. — Corti's rods and the hair-cells are covered by a special membrane (*o*), the **membrana reticularis** of Kölliker. The upper ends of

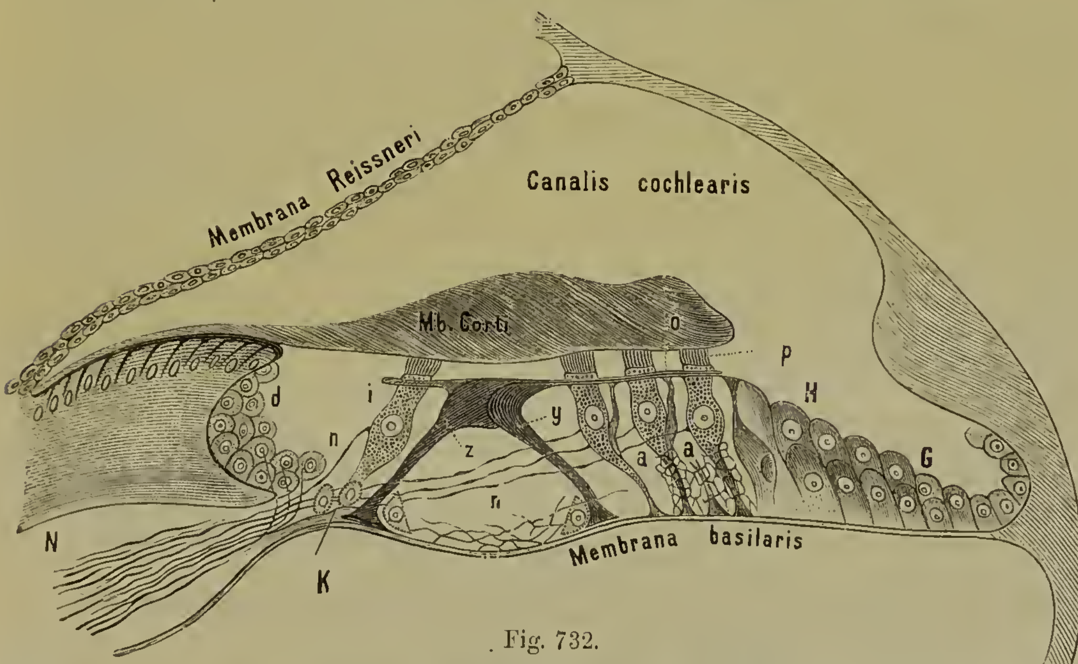


Fig. 732.

Scheme of the ductus cochlearis and the organ of Corti. N, cochlear nerve; K, inner, and P, outer hair-cells; *n*, nerve-fibrils terminating in P; *a*, *a*, supporting cells; *d*, cells in the sulcus spiralis; *z*, inner rod of Corti; Mb. Corti, membrane of Corti, or the membrana tectoria; *o*, the membrana reticularis; H, G, cells filling up the space near the outer wall.

the hair-cells, however, project through holes in this membrane, which consists of a kind of a cement-substance holding these parts together (*Lavdowsky*). [Springing from the outer end of the lamina spiralis, or crista spiralis, is the **membrana tectoria**, sometimes called the membrane of Corti. It is a well-defined structure, often fibrillated in appearance, and extends outwards over the organ of Corti.] Waldeyer regards it as a damping apparatus for this organ (fig. 732, Mb. Corti).

[**Basilar Membrane.**—Its breadth increases from the base to the apex of the cochlea. This fact is important in connection with the theory of the perception of tone. It is supposed that high notes are appreciated by structures in connection with the former, and low notes by the upper parts of the basilar membrane. In one case, recorded by Moos and Steinbrugge, a patient heard low notes only in

the right ear, and after death it was found that the auditory nerve in the first turn of the cochlea was atrophied.]

Intra-Labyrinthine Pressure.—The lymph within the labyrinth is under a certain pressure, every diminution of the pressure of the air in the tympanum is accompanied by a corresponding diminution of the intra-labyrinthine pressure, while conversely every increase of pressure is accompanied by an increase of the lymph-pressure (*F. Bezold*).

The **perilymph** of the inner ear flows away chiefly through the aqueductus cochleæ, in the circumference of the foramen jugulare, into the peripheral lymphatic system, which also takes up the cerebro-spinal fluid of the subarachnoid space, while a small part drains away to the sub-dural space through the internal auditory meatus. The **endolymph** flows through the arachnoid sheath of the N. acusticus into the subarachnoid space (*C. Hasse*).

[**Composition of Ear Fluids.**—**Perilymph** and **endolymph** are alkaline, and contain salts in about the same proportion as transudations. Perilymph contains 2·1 per cent. of solids, containing a trace of albumin, and more mucin and common salt. The endolymph is less viscid, and contains 1·5 per cent. of solids, and less mucin. **Otoliths** consist of 74·5–79 per cent. of inorganic matter, chiefly calcium carbonate. The organic matter is said to resemble mucin.]

414. AUDITORY PERCEPTIONS.—Every normal ear is able to distinguish **musical tones** and **noises.** Physical experiments prove that **tones** are produced when a vibrating elastic body executes **periodic** movements, *i.e.*, when the sounding body executes the same movement in equal intervals of time, as the vibrations of a string which has been plucked. A **noise** is produced by **non-periodic** movements, *i.e.*, when the sounding body executes unequal movements in equal intervals of time. [The non-periodic movements clash together on the ear, and produce dissonance, as when we strike the key-board of a piano at random.] This is readily proved by means of the siren. Suppose that there are forty holes in the rotatory disc of this instrument, placed at exactly the same distance from each other—on rotating the disc and directing a current of air against it, obviously with every rotation the air will be rarefied and condensed exactly forty times. Every two condensations and rarefactions are separated from each other by an *equal* interval of time. This arrangement yields a characteristic *musical tone* or note. If a similar disc with holes perforated in it at *unequal* distances be used, on air being forced against it, a whirring non-musical *noise* is produced, because the movements of the sounding body (the condensations and rarefactions of the air) are *non-periodic.* [The double siren of v. Helmholtz is an improved instrument for showing the same facts.]

The **normal ear** also distinguishes in **every tone three distinct factors**:—

[(1) Intensity or force :
(2) Pitch ;
(3) Quality, *timbre* or "*klang.*"]

1. The **intensity** of a tone depends upon the greater or lesser **amplitude** of the vibrations of the sounding body. It is well known that a vibrating string emits a feebler sound when its excursions are smaller. (The intensity of a sound corresponds to the *degree of illumination* or *brightness* in the case of the eye).

2. The **pitch** depends upon the **number of vibrations** which occur in a given time [or the length of time occupied by a single vibration]. This is proved by means of the siren. If the rotating disc have a series of forty holes at equal intervals, and another series of eighty equidistant from each other, on blowing a stream of air against the rotating disc we hear two sounds of unequal pitch, one being the octave of the other. (The perception of pitch corresponds to the *sensation of colour* in the case of the eye.)

3. The **quality** or **timbre** ("*Klangfarbe*") is peculiar to different sonorous bodies. [It is the peculiarity of a musical tone by which we are enabled to dis-

tinguish it as coming from a particular instrument, or from the human voice. Thus, the same note struck on a piano and sounded on a violin differs in quality or *timbre*.] It depends upon the *peculiar form of the vibration*, or the form of the wave of the sonorous body. (There is no analogous sensation in the case of light.)

I. Perception of Pitch.—By means of the organ of hearing, we can determine that different tones have a different pitch. In the so-called musical scale, or gamut, this difference is very marked to a normal ear. But in the scale there are again four tones, which, when they are sounded together, cause in a normal ear the sensation of an agreeable sound, which once heard can readily be reproduced. This is the tone of the so-called **accord**, Triad, or Common Chord, consisting of the 1st, 3rd, and 5th tones of the scale, to which the 8th tone or octave is added. We have next to determine the pitch of the tones of the chord, and then that of the other tones of the scale. The siren is used for the fundamental experiment, from which the others can easily be calculated. Four concentric circles are drawn upon the rotatory disc of the siren; the inner circle contains 40 holes, the second 50, the third 60, and the outer 80—all the holes being at equal distances from each other. If the disc be rotated, and air forced against each series of holes *in turn*, we distinguish successively the four tones of the *accord* (major chord with its octave); when all the four series are blown upon *simultaneously*, we hear in complete purity the major chord itself. The *relative number of the holes* in the four series indicates in the simplest manner the relative pitch of the tones of the major chord. While one revolution of the disc is necessary to produce the *fundamental ground-tone* (key-note or tonic) with 40 condensations and rarefactions of the air—in order to produce the **octave**, we must have double the number of condensations and rarefactions during one revolution in the same time. Thus, the relation of the number of vibrations of the Ground-tone or Tonic to the Octave next above it, is 1 : 2. In the second series we have 50 holes, which causes the pitch of the **third**; hence, the relation of the Ground-tone to the Third in this case is 40 : 50, or 1 : $1\frac{1}{4}=\frac{5}{4}$, *i.e.*, for every vibration of the Ground-tone there are $\frac{5}{4}$ vibrations in the Third. In the third series are 60 holes, which, when blown upon, yield the **fifth**; hence, the ratio of the Ground-tone to the Fifth in our disc is 40 : 60, or 1 : $1\frac{1}{2}=\frac{3}{2}$. In the same way we can estimate the pitch of the Fourth tone, and we find that the number of vibrations of the First, Third, Fifth, and Octave are to each other as 1 : $\frac{5}{4}$: $\frac{3}{2}$: 2.

The **minor chord** is quite as characteristic to a normal ear as the major. It is distinguished essentially from the latter by its Third being half a tone lower. We can easily imitate it by the siren, as the *Minor Third* consists of a number of vibrations which stand to the ground-tone as 6 : 5, *i.e.*, if 5 vibrations occur in a given time in the Ground-tone, then 6 occur in the Minor Third; its vibration number, therefore, is $\frac{6}{5}$.

From these relations of the Major and Minor common chords, we may calculate the relative tones in the scale, and we must remember that the Octave of a tone always yields the fullest and most complete harmony. It is evident that as the Major Third, and Minor Third, and the Fifth harmonise with the fundamental Ground-tone or key-note, they must also harmonise with the Octave of the key-note. We obtain from the Major Third with the number of vibrations $\frac{5}{4}$, the Minor Sixth $\frac{5}{8}$, from the Minor Third with $\frac{6}{5}$, the Major Sixth $=(\frac{6}{10}=)\ \frac{3}{5}$; from the Fifth with $\frac{3}{2}$, the Fourth $=\frac{3}{4}$. These relations are known as the "Inversions of the intervals." These relations of the tones are, collectively, the consonant intervals of the scale. The dissonant stages, or discords, of the scale can be obtained as follows:—Suppose that we have the Ground-tone or key-note C, with the number of vibrations = 1, the Third E $=\frac{5}{4}$, the Fifth G $=\frac{3}{2}$, and the Octave = 2, we then derive from the Fifth or Dominant G a Major chord—this is G, B, D'. The relative number of vibrations of these 3 tones is the same as in the Major chord of C', C, E, G. Hence, the number of vibrations of G : B is as C : E. When we substitute the values we obtain $\frac{3}{2}$: B = 1 : $\frac{5}{4}$—*i.e.*, B $=\frac{15}{8}$. But D' : B = G : E; so that D : $\frac{15}{8}=\frac{3}{2}:\frac{5}{4}$, *i.e.*, D' $=\frac{18}{8}$, or an octave lower, we have D $=\frac{9}{8}$. Deduce from F (subdominant) a Major chord, F, A, C'. The relation of A : C' = E : G, or A : 2 $=\frac{5}{4}:\frac{3}{2}$, *i.e.*, A $=\frac{5}{3}$. Lastly, F : A = C : E, or F : $\frac{5}{3}$ = 1 : $\frac{5}{4}$, *i.e.*, F $=\frac{4}{3}$. So that all the tones of the scale have the following number of vibrations:—I., C = 1; II., D $=\frac{9}{8}$; III., E $=\frac{5}{4}$; IV., F $=\frac{4}{3}$; V., G $=\frac{3}{2}$; VI.; A $=\frac{5}{3}$; VII., B $=\frac{15}{8}$; VIII., C' = 2.

Conventional Estimate of Pitch.—Conventionally, the pitch or concert-pitch of the note, *a*, is taken at 440 vibrations in the second (*Scheibler*, 1834), although in France it is taken at 435 vibrations per second. From this we can estimate the absolute number of vibrations for the tones of the scale:—C = 33, D = 37·125, E = 41·25, F = 44, G = 49·5, A = 55, B = 61·875 vibrations. The number of vibrations of the next highest octave is found at once by multiplying these numbers by 2.

Musical Notes.—The **lowest notes** used in music are the double-bass, E, with 41·25 vibrations, pianoforte C with 33, grand piano A with 27·5, and organ C with 16·5. The **highest notes** in music are the pianoforte c^{v} with 4224, and d^{v} on the piccolo-flute, with 4752 vibrations per second.

Limits of Auditory Perception.—According to Preyer, the limit of the percep-

tion of the lowest audible tone lies between 16 and 23 vibrations per second, and e^{viii} with 40,960 vibrations as the highest audible tone; so that this embraces about $11\frac{1}{2}$ octaves.

[**Audibility of Shrill Notes.**—This varies very greatly in different persons (*Wollaston*). There is a remarkable falling off of the power as age advances (*Galton*). For testing this Galton uses a small whistle made of a brass tube, with a diameter of less than $\frac{1}{10}$th of an inch (fig. 733). A plug is fitted at the lower end to lengthen or shorten the tube, whereby the pitch of the note is altered. Amongst animals Galton finds none superior to cats in the power of hearing shrill sounds, and he attributes this "to differentiation by natural selection amongst these animals until they have the power of hearing all the high notes made by mice and other little creatures they have to catch."]

Fig. 733. Galton's Whistle.

Variations in Auditory Perception.—It is rare to find that tones produced by more than 35,000 vibrations per second are heard. When the tensor tympani is contracted, the perception may be increased for tones 3000 to 5000 vibrations higher, but rarely more. **Pathologically**, the perception for high notes may be abnormally acute—(1) When the tension of the sound-conducting apparatus generally is increased. (2) By elimination of the sound-conducting apparatus of the middle ear, which offers greater or less resistance to the propagation of very high notes, as perforation of the membrana tympani, or loss of the incus and malleus. In these cases, the stapes is directly set in vibration by the sound-waves, when tones up to 80,000 vibrations have been perceived. Diminished tension of the sound-conducting apparatus causes diminution of the perception for high tones (*Blake*).

A smaller number of vibrations than 16 per second (as in the organ) are no longer heard as a tone, but as single dull impulses. The tones that are produced beyond the highest audible note, as by stroking small tuning-forks with a violin bow, are also no longer heard as tones, but they cause a painful cutting kind of impression in the ear. In the musical scale the range is, approximately, from C of the first octave with 16·5 vibrations to c, the eighth octave.

Comparison of Ear and Eye.—In comparing the perception of the eye with that of the ear, we see at once that the range of accommodation of the ear is much greater. Red has 456 billions of vibrations per second, while the visible violet has but 667, so that the eye only takes cognisance of vibrations which do not form even one octave.

Lowest Audible Tone.—As to the *smallest* number of successive vibrations which the ear can perceive as a sensation of tone, Savart and Pfaundler considered that two would suffice. If, however, we exclude in our experiments the possibility of the occurrence of overtones, 4 to 8 (*Mach*) or even 16 to 20 vibrations (*F. Auerbach, Kohlrausch*) are necessary to produce a characteristic tone.

When tones succeed each other rapidly, they are still perceived as distinct, when at least 0·1 second intervenes between two successive tones (*v. Helmholtz*); if they follow each other more rapidly, they fuse with each other, although a short-time interval is sufficient for many musical tones.

By the term, "*fineness of the ear*," or, as we say, a "good ear," is meant the capacity of distinguishing from each other, as different, two tones of nearly the same number of vibrations. This power can be greatly increased by practice, so that musicians can distinguish tones that differ in pitch by only $\frac{1}{500}$, or even $\frac{1}{1200}$ of their vibrations.

With regard to the **time-sense**, it is found that beats are more precisely perceived by the ear than by the other sense organs (*Höring, Mach*).

Pathological.—According to Lucae, there are some ears that are better adapted for hearing *low* notes and others for *high* notes. Both conditions are disadvantageous for hearing speech. Those who hear low notes best hear the highest consonants imperfectly. The low notes are heard abnormally loud in rheumatic facial paralysis, while the high tones are heard abnormally loud in cases of loss of the membrana tympani, incus, and malleus. The stapedius is in full action, whereby the highest tones are heard louder at the expense of the lower notes. Many persons with normal hearing hear a tone higher with one ear than with the other. This condition is called **diplacusis binauralis**. In rare cases, sudden loss of the perception of certain tones has been observed, *e.g.*, the **bass-deafness** of Moos. In a case described by Magnus, the tones d^{I}, b^{I}, were not heard (§ 316).

II. **Perception of the Intensity of Tone.**—The *intensity* of a tone depends upon the *amplitude of the vibrations* of the sounding body. The intensity of the tone is proportional to the

square of the amplitude of vibration of the sounding body, *i.e.*, with 2, 3, or 4 times the amplitude the intensity of the tone is 4, 9, 16 times as strong. As sonorous vibrations are communicated to our ears by the wave-movements of the air, it is evident that the tones must become less and less intense the further we are from the source of the sound. The intensity of the sound is inversely proportional to the square of the distance of the source of the sound from the ear.

Tests.—1. Place a watch horizontally near the ear, and test how close it may be brought to the ear, and also how far it may be removed, and still its sounds be heard. Measure the distance. 2. Hard uses a small hammer suspended like a pendulum, and allowed to fall upon a hard surface. 3. Balls of different weights are allowed to fall from varying heights upon a plate. In this case the intensity of the sound is proportional to the product of the weight of the ball into the height it falls.

As to the **limits** of the perception of the intensity of a tone, it is found that a spherule weighing 1 milligram, and falling from a height of 1 mm. upon a glass plate, is heard at a distance of 5 centimetres (*Schafhäutl*).

415. **PERCEPTION OF QUALITY — VOWELS.** — By the term **quality** ("Klangfarbe"), *musical colour* or **timbre**, is understood a peculiar character of the tone, by which it can be distinguished apart from its pitch and intensity. Thus, a flute, horn, violin, and the human voice may all sound the same note with equal intensity, and yet all the four are distinguished at once by their specific quality. Wherein lies the essence ("Wesen") of tone-colour? The investigations of v. Helmholtz have proved that, amongst mechanisms which produce tones, only those that produce pendulum-like vibrations, *i.e.*, the to-and-fro vibrations of a metallic rod with one end fixed, and tuning-forks, execute simple pendulum-like vibrations. This can be shown by making a tuning-fork write off its vibrations on a recording surface, when a completely uniform wave-line, with equal elevations and depressions is noted. The term "**tone**" is restricted to those sounds, hardly ever occurring in nature, which are due to simple pendulum-like vibrations.

Other investigations have shown that the tones of musical instruments and of the human voice, all of which have a characteristic quality of their own, are composed of many single simple tones. Amongst these *one* is characterised by its intensity, and at the same time it determines the pitch of the whole compound musical "tone-picture." This is called the **fundamental tone** or key-note. The other weaker tones which, as it were, spring from and are mingled with this, vary in different instruments both in intensity and number. They are "**upper tones**," and their vibrations are always some multiple—2, 3, 4, 5 .... times—of the fundamental tone or key-note. In general, we say that all those outbursts of sound which embrace numerous strong upper tones, especially of high pitch, in addition to the fundamental tone, are characterised by a sharp, piercing, and rough quality, such as emanates from a trumpet or clarionet, and that conversely the quality is characterised by mildness and softness when the overtones are few, feeble, and low, *e.g.*, such as are produced by the flute. It requires a well-trained musical ear to distinguish, in an instrumental burst, the overtones apart from the fundamental tone. But this is very easily done with the aid of **resonators** (fig. 735). These consist of spherical or funnel-shaped hollow bodies, made of brass or some other substance, which, by means of a short tube, can be placed in the outer ear. If a resonator be placed in the ear, we can hear the feeblest overtone of the same number of vibrations as the fundamental tone. Thus, musical instruments are distinguished by the number intensity, and pitch of the overtones which they produce. A vibrating metallic rod and a tuning-fork have no overtones; they only give the fundamental tone. As already mentioned, the term *simple* **tone** is applied to sounds due to simple pendulum-like vibrations, while a

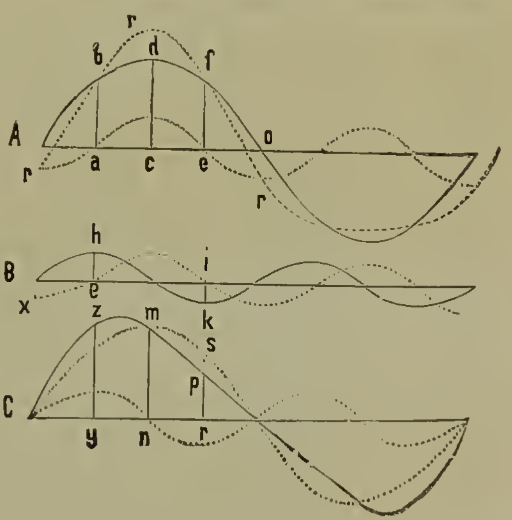


Fig. 734.

Curves of a musical tone obtained by compounding the curve of a fundamental tone with that of its overtones.

sound composed of a fundamental tone and overtones is called a "klang" or *compound* musical tone.

Vibration Curve of a Musical Tone.—When we remember that a musical tone or clang consists of a fundamental tone, and a number of overtones of a certain intensity, which determine its quality, then we ought to be able to construct geometrically the vibration curve of the musical tone. Let A represent the vibration curve of the fundamental tone, and B that of the first moderately weak overtone (fig. 734). The combination of these two curves is obtained simply by computing the height of the ordinates, whereby the ordinates of the overtone curve, lying above the abscissa or horizontal line, are added to the fundamental tone curve, while those of the ordinates below the line are subtracted from it. Thus we obtain the curve C, which is not a simple pendulum-like curve, but one which corresponds to an *unsteady* movement. A new curve of the second overtone may be added to C, and so on. The result of all these combinations is that the vibration curves corresponding to the compound musical tones are *unsteady* periodic curves. All these curves must, of course, vary with the number and pitch of the compounded overtone curves.

Displacement of the Phases.—The form of the vibration of one and the same musical tone may vary very greatly if, in compounding the curves A and B, the curve B is only slightly displaced laterally. If B is displaced so that the hollow of the wave r falls under A, the addition of both curves yields the curve r, r, r, with small elevations and broad valleys. If B be displaced still further, until the elevation of the wave, h, coincides with A, we obtain still another form, so that by displacement of the *phases* of the wave-motions of the compounded simple pendulum-like vibrations, we obtain numerous different forms of the same musical tone. The displacement of the phases, however, has no effect on the ear.

The general result of these observations, and those of Fourier, is that the quality of a musical tone depends upon the characteristic form of the vibratory movement.

Analysis of Vowels.—The human voice represents a reed instrument with vibrating elastic membranes, the vocal cords (§ 312). In uttering the various vowels the mouth assumes a characteristic form, so that its cavity has a certain fundamental tone peculiar to itself. Thus, to the fundamental tone of a certain pitch produced within the larynx, there are added certain overtones, which communicate to the laryngeal tone the vocal or vowel quality. Hence, a vowel is the timbre or quality of a musical tone which is produced in the larynx. The quality depends upon the number, intensity, and pitch of the overtones, and the latter, again, depend on the configuration of the "vocal cavity" in uttering the different vowels (§ 317).

Suppose a person to sing the vowels one after the other on a special note, *e.g.*, b ♭, we can, with the aid of resonators, determine the overtones, and in what intensity they are mixed with the fundamental tone, b ♭, to give the characteristic quality. According to v. Helmholtz, when we sound the vowels on b ♭, for each of the three vowels, *one* overtone is specially characteristic for A–b$''$ ♭; for O–b$'$ ♭; for U–f. The other vowels and the diphthongs have each *two* specially characteristic overtones, because in these cases the mouth is so shaped that the posterior larger cavity, and also the anterior narrower part, each yields a special tone (§ 316, I. and E). These two overtones are for E–B$''$ ♭ and f$'$; for I–d^{iv} and f; for Ä–g and d$''$; for Ö–e$'''$ ♯ and f$'$; for Ü–g$''$ and f. These, however, are only the special upper tones. There are many more upper tones, but they are not so prominent.

Artificial Vowels.—Just as it is possible to analyse a vowel into its fundamental tone and its upper tones, it is possible to compound tones to produce the vowels by simultaneously sounding the fundamental tone and the corresponding upper tones. (1) A vowel is produced simply by singing loudly a vowel, *e.g.*, A, upon a certain note against the free strings of an open piano, whilst by the pedal the damper is kept raised. As soon as we stop singing, the characteristic vowel is sounded by the strings of the piano. The voice sets into sympathetic vibration all those strings whose overtones (in addition to the fundamental tone) occur in the vocal compound tone, so that they vibrate for a time after the voice ceases (*v. Helmholtz*). (2) The vowel apparatus devised by v. Helmholtz consists of numerous tuning-forks, which are kept vibrating by means of electro-magnets. The lowest tuning-fork gives the fundamental tone, B ♭, and the others the overtones. A resonator is placed in front of each tuning-fork, and the distance between the two can be varied at pleasure. The resonators can be opened and closed by a lid passing in front of their openings. When the resonator is closed, we cannot hear the tone emitted by the tuning-fork placed in front of it; but when one or more resonators are opened the tone is heard distinctly, and it is louder the more the resonator is opened. By means of a series of keys, like the keys of a pianoforte, we can rapidly open and close the resonators at will, and thus combine various overtones with the fundamental tone so as to produce vowels with different qualities. V. Helmholtz makes the following compositions:—U = B ♭ with b ♭ weak and f$'$; O = damped B ♭ with b$'$ ♭ strong and weaker b ♭, f, d$'$; A = b ♭ (fundamental tone) with moderately strong b$'$ ♭ and f$'$, and strong b$''$ ♭ and d$''$; A = b ♭ (fundamental tone) with b$'$ ♭ and f$''$ somewhat stronger than for A, d strong, b$''$ ♭ weaker, d and f$''$ as strong as possible; E = b ♭ (as fundamental tone) moderately strong, with b$'$ ♭ and f moderate also, and f$''$, a$''$ ♭, and b$'''$ ♭, as strong as possible; I could not be produced.

In **Appunn's apparatus**, the fundamental tone and the overtones are produced by means of

organ pipes, whose notes can be combined to produce the vowels, but it is not so good as the

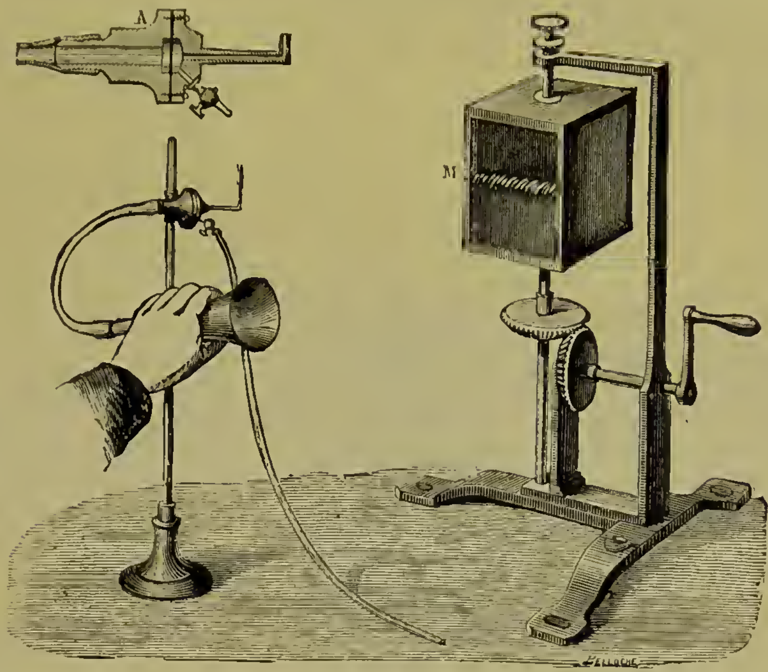


Fig. 735.
Koenig's manometric capsule (A) and mirror (M) (*Koenig*).

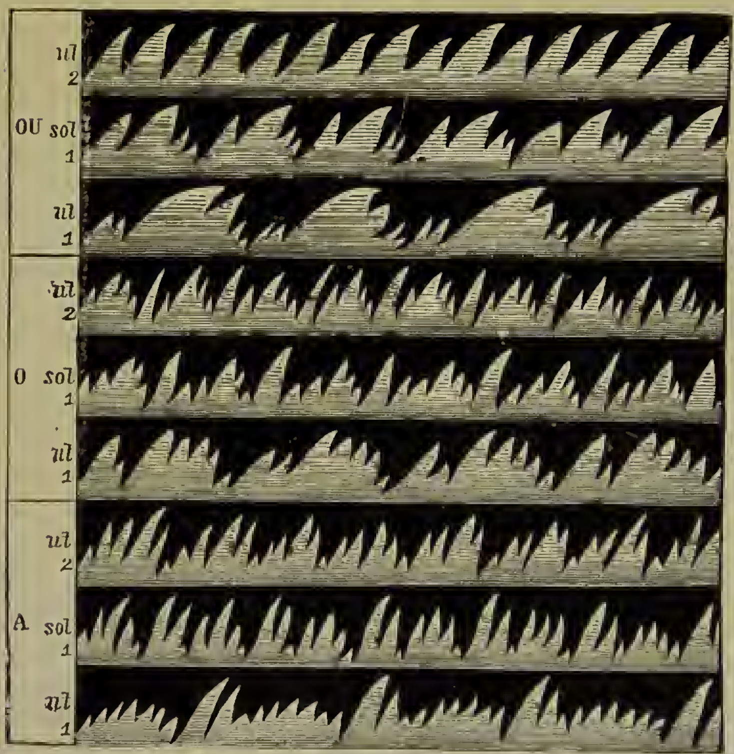


Fig. 736.
Flame-pictures of the vowels OU, O, and A (*Koenig*).

tuning-forks, since the organ pipes do not yield simple tones, but nevertheless some of the vowels can be admirably reproduced with this apparatus.

Edison's Phonograph.—If we utter the vowels against a delicate membrane stretched over the end of a hollow cylinder, and if a writing style be fixed to the centre of the membrane, and the style be so arranged that it can write or record its movements on a piece of soft tinfoil arranged on a revolving apparatus, then the vowel curve is stamped as it were upon the tinfoil. If the style now be made to touch the tinfoil while the latter is moved, then the style is moved—it moves the membrane, and we hear distinctly by resonance the vowel sound reproduced.

[**Koenig's Manometric Flames.**—By means of this apparatus the quality of the vowel sounds is easily shown. It consists of a small wooden capsule, A, divided into two compartments by a piece of thin sheet india-rubber. Ordinary gas passes into the chamber on one side of the membrane, through the stop-cock, and it is lighted at a small burner. To the other compartment is attached a wider tube with a mouthpiece. The whole is fixed on a stand, and near it is placed a four-sided rotating mirror, M, as suggested by Wheatstone (fig. 735). On speaking or singing a vowel into the mouthpiece, and rotating the mirror, a toothed or zigzag flame-picture is obtained in the mirror. The form of the flame-picture is characteristic for each vowel, and varies of course with the pitch.] [Fig. 736 shows the form of the flame-picture obtained in the rotating mirror when the vowels, OU, O, A, are sung at a pitch of ut_1, sol_1, and ut_2. This series shows how they differ in quality.]

[Koenig has also invented the apparatus for **analysing any compound tone** whose fundamental tone is UT_2 (fig. 737). It consists of a series of resonators, from UT_2 to UT_5, fixed in an iron frame. Each resonator is connected with its special flame, which is pictured in a long narrow, square rotating mirror. If a tuning-fork UT_2 be sounded, only the flame UT_2 is affected, and so on with each tuning-fork of the harmonic series. Suppose a compound note containing the fundamental tone UT_2, and its harmonics be sounded, then the flame of UT_2, and those of the other harmonics in the note are also affected, so that the tone can be analysed optically. The same may be done with the vowels.]

416. LABYRINTH DURING HEARING.—If we ask what rôle the ear plays in the perception of the **quality** of sounds, then we must assume that, just as with the help of resonators a musical note can be resolved into its fundamental tone and overtones, so the ear is capable of performing such an analysis. The ear resolves the complicated wave-forms of musical tones into their components. These components it perceives as tones harmonious with each other; with marked attention each is perceived singly, so that the ear distinguishes as different tone-colours only different combinations of these simple tone-sensations. The resolution of complex vibrations, due to quality, into simple pendulum-like vibrations is a characteristic function of the ear. What apparatus in the ear is capable of doing this? If we sing vigorously—*e.g.*, the musical vowel A on a definite note, say b ♭—against the strings of an open pianoforte while the damper is raised, then we cause all those strings, and *only* those, to vibrate sympathetically, which are contained in the vowel so sung. We must, therefore, assume that an analogous sympathetic apparatus occurs in the ear, which is tuned, as it were, for different pitches, and which will vibrate sympathetically like the strings of a pianoforte. "If we could so connect every string of a piano with a nerve-fibre that the nerve-fibre would be excited and perceived as often as the string vibrated, then, as is actually the case in the ear, every musical note which affected the instrument would excite a series of sensations exactly corresponding to the pendulum-like vibrations into which the original movements of the air can be resolved; and thus the existence of each individual overtone would be exactly perceived, as is actually the case with the ear. The perception of tones of different pitch would under these circumstances depend upon different nerve-fibres, and hence would occur quite independently of each other. Microscopic investigation shows that there are somewhat similar structures in the ear. The free ends of all the nerves-fibres are connected with small elastic particles which we must assume are set into sympathetic vibration by the sound-waves" (*v. Helmholtz*).

Resolution by the Cochlea.—Formerly v. Helmholtz considered the rods of Corti to be the apparatus that vibrated and stimulated the terminations of the nerves. But, as **birds** and **amphibians**, which certainly can distinguish musical notes, have **no rods** (*Hasse*), the *stretched radial fibres of the membrana basilaris*, on which the organ of Corti is placed, and which are shortest in the first turn of the cochlea,

becoming longer towards the apex of the cochlea, are now regarded as the vibrating threads (*Hensen*). Thus, a string-like fibre of the membrana basilaris, which is capable of vibrating, corresponds to every possible simple tone. According to Hensen, the hairs of the labyrinth, which are of unequal length, may serve this purpose. Destruction of the apex of the cochlea causes deafness to deeper tones (*Baginsky*).

[**Hensen's Experiments.**—That the hairs in connection with the hair-cells vibrate to a particular note is also rendered probable by the experiments of Hensen on the crustacean *Mysis*. He found that certain of the minute hairs (auditory hairs) in the auditory organ of this animal, situate at the base of the antennæ, vibrated when certain tones were sounded on a keyed horn. The movements of the hairs were observed by a low-power microscope. In mammals, however, there is a difficulty, as the hairs attached to the cells appear to be all about the same length. We must not forget that the perception of sound is a mental act.]

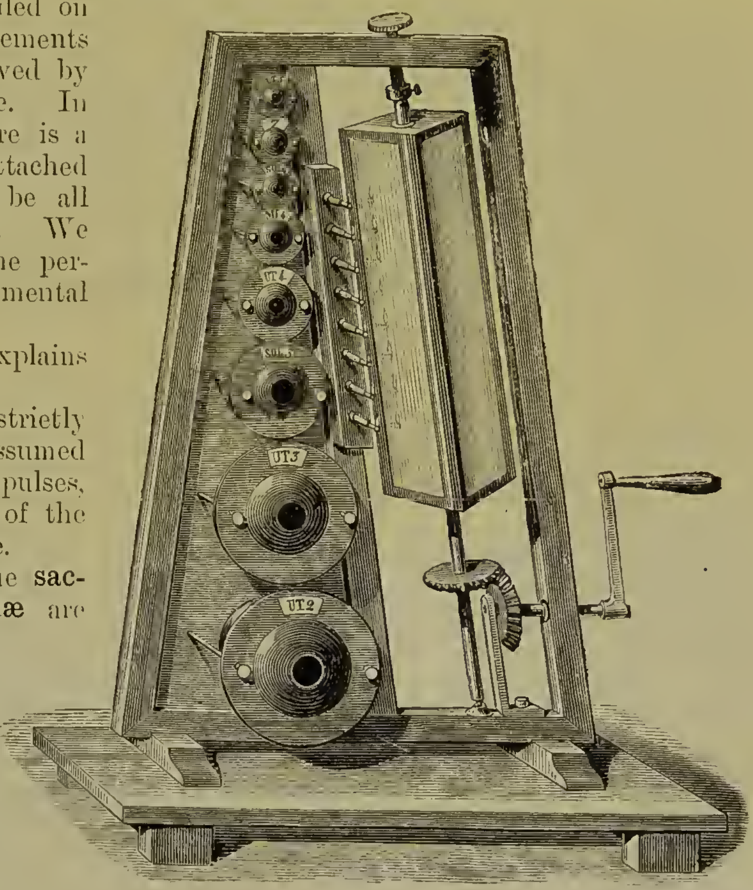


Fig. 737.
Koenig's apparatus for analysing a compound tone with the fundamental tone UT_2.

This assumption also explains the perception of *noises*.

Of **noises** in the strictly physical sense, it is assumed that they, like single impulses, are perceived by the aid of the saccules and the ampullæ.

It is assumed that the **saccules** and the **ampullæ** are concerned in the general perception of hearing, *i.e.*, of shocks communicated to the auditory nerve (by impulses and noises); while by the **cochlea** we estimate the pitch and depth of the vibrations, and musical character of the vibrations produced by tones. The relation of the **semicircular canals** to the **equilibrium** of the body is referred to in § 350.

417. SIMULTANEOUS ACTION OF TWO TONES—HARMONY—BEATS —DISCORDS—DIFFERENTIAL TONES.

—When *two* tones of different pitch fall upon the ear simultaneously, they cause different sensations according to the difference in pitch.

1. **Consonance.**—If the number of vibrations of the two tones is in the ratio of simple multiples, as 1 : 2 : 3 : 4, so that when the low notes make one vibration the higher one makes 2 : 3 or 4 . . . . then we experience a sensation of complete harmony or concord.

2. **Interference.**—If, however, the two tones do not stand to each other in the relation of simple multiples, then when both tones are sounded simultaneously

interference takes place. The hollows of the one sound-wave can no longer coincide with the hollows of the other, and the crests with the crests, but, corresponding to the difference of number of vibrations of both curves, sometimes a wave-crest must coincide with a wave-hollow. Hence, when wave-crest meets wave-crest, there must be an *increase* in the strength of the tone, and when a hollow coincides with a crest, the sound must be weakened. Thus we obtain the impression of those variations in tone intensity which have been called "**beats.**"

The number of vibrations is of course always equal to the difference of the number of vibrations of both tones. The beats are perceived most distinctly when two organ tones of low pitch are sounded together in unison, but slightly out of tune. Suppose we take two organ pipes with 33 vibrations per second, and so alter one pipe that it gives 34 vibrations per second, then *one* distinct beat will be heard every second. The beats are heard more frequently the greater the difference between the number of vibrations of the two tones.

Successive Beats.—The beats, however, produce very different impressions upon the ear according to the rapidity with which they succeed each other.

1. **Isolated Beats.**—When they occur at long intervals, we may perceive them as completely isolated, but single intensifications of the sound with subsequent enfeeblement, so that they give rise to the impression of *isolated beats.*

2. **Dissonance.**—When the beats occur more rapidly they cause a continuous disagreeable whirring impression which is spoken of as *dissonance*, or an unharmonious sensation. The greatest degree of unpleasant painful dissonance occurs when there are 33 beats per second.

3. **Harmony.**—If the beats take place more rapidly than 33 times per second, the sensation of dissonance gradually diminishes, and it does so the more rapidly the beats occur. The sensation passes gradually from moderately inharmonious relations (which in music have to be resolved by certain laws) towards consonance or harmony. The tone relations are successively the Second, Seventh, Minor Third, Minor Sixth, Major Third, Major Sixth, Fourth, and Fifth.

4. **Effect of the Musical Tones** ("*Klange*").—Two musical "klangs," or compound tones, falling on the ear simultaneously, produce a result similar to that of two simple tones; but in this case we have to deal not only with the two fundamental tones, but also with the overtones. Hence the degree of dissonance of two musical tones is the more pronounced the more the fundamental tones and the overtones (and the "differential" tones) produce beats which number about 33 per second.

5. **Differential Tones.**—Lastly two "klangs," or two simple musical tones sounding simultaneously, may give rise to *new tones* when they are uniformly and simultaneously sounding in corresponding intensity. We can hear, if we listen attentively, a third new tone, whose number of vibrations corresponds to the difference between the two primary tones, and hence it is called a "*differential tone.*"

Summational Tones.—It was formerly supposed that new tones could arise from the summation or *addition* of their number of vibrations, but it has been shown that these tones are in reality differential tones of a high order (*Appunn, Preyer*).

418. PERCEPTION OF SOUND — OBJECTIVE AND SUBJECTIVE AUDITION—AFTER-SENSATION.—**Objective and Auditory Perceptions.**—When the stimulation of the terminations of the nerves of the labyrinth is referred to the outer world, then we have *objective auditory perceptions.* Such stimulations are only referred to the outer world as are conveyed to the membrana tympani by vibrations of the air, as is shown by the fact that if the head be immersed in water, and the auditory meatuses be filled thereby, we hear all the vibrations as if they occurred within our head itself (*Ed. Weber*), and the same is the case with our own voice, as well as with the sound-waves conducted through the bones of the head, when both ears are firmly plugged.

Perception of Direction.—As to the perception of the direction whence sound comes, we obtain some information from the relation of both meatuses to the source of the sound, especially if we turn the head in the supposed direction of the sound. We distinguish more easily the direction from which noises mixed with musical tones come than that of tones (*Rayleigh*). When both ears are stimulated equally, we refer the source of the sound to the middle line anteriorly, but when one ear is stimulated more strongly than the other, we refer the source of the sound more to one side (*Kessel*). The position of the ear-muscles, which perhaps act like an ear-funnel, is important. According to Ed. Weber, it is more difficult to determine the direction of sound when the ears are firmly fixed to the side of the head. Further, if we place the hollow of both hands in front of the ear, so as to form an open cavity behind them, we are apt to suppose that a sounding body placed in front is behind us. The semicircular canals are said also to be concerned, as sound coming from a certain direction must always excite one canal more than the others. Thus, the left horizontal canal is most stimulated by horizontal sound-waves coming from the left (*Preyer*). Other observers assert that the membrana tympani localises the sound, as only certain parts of it are affected by the sound-waves.

The **distance** of a sound is judged of partly by the *intensity* or *loudness* of the sound, such as we have learned to estimate from sound at a known distance. But still we are subject to many misconceptions in this respect.

Amongst **subjective auditory sensations** are the *after-vibrations*, especially of intense and continued musical tones; the **tinnitus aurium** (p. 741), which often accompanies abnormal movements of the blood in the ear, may be due to a mechanical stimulation of the auditory fibres, perhaps by the blood-stream (*Brenner*).

[**Drugs.**—Cannabis indica seems to act on the hearing centre, giving rise to subjective sounds; the hearing is rendered more acute by strychnin; while quinine and sodic salicylate in large doses cause ringing in the ears (*Brunton*).]

Entotical perceptions, which are due to causes within the ear itself, are such as hearing the *pulse-beats* in the surrounding arteries, and the rushing sound of the blood, which is especially strong when there is increased resonance of the ear (as when the meatus or tympanum is closed, or when fluid accumulates in the latter), during increased cardiac action, or in hyperæsthesia of the auditory nerve (*Brenner*). Sometimes there is a cracking noise in the maxillary articulation, the noise produced by traction of the muscles on the Eustachian tube (§ 411), and when air is forced into the latter, or when the membrana tympani is forced outwards or inwards (§ 350).

Fatigue.—The ear after a time becomes fatigued, either for one tone or for a series of tones which have acted on it, while the perceptive activity is not affected for other tones. Complete recovery, however, takes place in a few seconds (*Urbantschitsch*).

Auditory After-Sensations.—(1) Those that correspond to *positive* after-sensations, where the after-sensation is so closely connected with the original tone that both appear to be continuous. (2) There are some after-sensations, where a pause intervenes between the end of the objective and the beginning of the subjective tone (*Urbantschitsch*). (3) There seems also to be a form corresponding to *negative* after-images.

In some persons, the perception of a tone is accompanied by the occurrence of subjective colours, of the sensation of light, *e.g.*, the sound of a trumpet, accompanied by the sensation of yellow. More seldom visual sensations of this kind are observed when the nerves of taste, smell, or touch are excited (*Nussbaumer*, *Lehmann and Bleuler*). It is more common to find that an intense sharp sound is accompanied by an associated sensation of the sensory nerves. Thus many people experience a cold shudder when a slate pencil is drawn in a peculiar manner across a slate.

[**Colour Associations.**—Colour is in some persons instantaneously associated with sound, and Galton remarks that it is rather common in children, although in an ill-developed degree, and the tendency seems to be very hereditary. Sometimes a particular colour is associated with a particular letter, vowel sounds particularly evoking colours. Galton has given coloured representations of these colour associations, and he points out their relation to what he calls **number-forms**, or the association of certain forms with certain numbers.]

An auditory impulse communicated to *one* ear at the same time often causes an increase in the auditory function of the *other* ear, in consequence of the stimulation of the auditory centres of *both* sides (*Urbantschitsch*, *Eitelberg*).

Other Stimuli.—The auditory apparatus, besides being excited by sound-waves, is also

affected by heterologous stimuli. It is estimated *mechanically* by a sudden blow on the ear. The effects of *electricity* and pathological conditions are referred to in § 350.

419. **COMPARATIVE—HISTORICAL.**—The lowest fishes, the cyclostomata (Petromyzon), have a saccule provided with auditory hairs containing otoliths, and communicating with two semicircular canals, while the myxinoids have only one semicircular canal. Most of the other fishes, however, have a utricle communicating with three semicircular canals. In the carp, prolongations of the labyrinth communicate with the swimming-bladder. In **amphibia**, the structure of the labyrinth is somewhat like that in fishes, but the cochlea is not typically developed. Most amphibia, except the frog, are devoid of a membrana tympani. Only the fenestra ovalis (not the rotunda) exists, and it is connected in the frog by three ossicles with the freely-exposed membrana tympani. Amongst **reptiles** the appendix to the saccule corresponding to the cochlea begins to be prominent. In the tortoise it is saccular, but in the crocodile it is longer, and somewhat curved and dilated at the end. In all reptiles the fenestra rotunda is developed, whereby the cochlea is connected with the labyrinth. In crocodiles and **birds**, the cochlea is divided into a scala vestibuli and S. tympani. Snakes are devoid of a tympanic cavity. In birds both saccules (fig. 728, IV, U S) are united (*Hasse*), the canal of the cochlea (U C), which is connected by means of a fine tube (C) with the saccule, is larger, and shows indications of a spiral arrangement, and has a flask-like blind end, the lagena (L). The auditory ossicles in reptiles and birds are reduced to *one* column-like rod, corresponding to the stapes, and called the **columella**. The lowest **mammals** (Echidna) have structures very like those of birds, while the higher mammals have the same type as in man (fig. 728, III). The Eustachian tube is always open in the whale.

Amongst **invertebrata**, the auditory organ is very simple in medusæ and mollusca. It is merely a bladder filled with fluid, with the auditory nerves provided with the ganglia in its walls. Hair-cells occur in the interior, provided with one or more otoliths. Hensen observed that in some of the annulosa, when sound was conducted into the water, some of the auditory bristles vibrated, being adapted for special tones. In cephalopoda, we distinguish the first differentiation into a membranous and cartilaginous labyrinth.

Historical.—Empedocles (473 B.C.) referred auditory impressions to the cochlea. The Hippocratic School was acquainted with the tympanum, and Aristotle (384 B.C.) with the Eustachian tube. Vesalius (1561) described the tensor tympani; Gardanus (1560) the conduction through the bones of the head; while Fallopius (1561) described the vestibule, the semicircular canals, chorda tympani, the two fenestræ, the cochlea, and the aqueduct. Eustachius († 1570) described the modiolus, the lamina spiralis of the cochlea, the Eustachian tube, as well as the muscles of the ear; Plater the ampullæ (1583); Casseri (1600) the lamina spiralis membranacea. Sylvius (1667) discovered the ossicle called by his name; Vesling (1641) the stapedius. Mersenne (1618) was acquainted with overtones; Gassendus (1658) experimented on the conduction of sound. Acoustics were greatly advanced by the work of Chladni (1802). The most recent and largest work on the ear in vertebrates is by G. Retzius (1881-84).

The Sense of Smell.

420. **STRUCTURE OF THE ORGAN OF SMELL.**—**Regio Olfactoria**—The area of the distribution of the olfactory nerve is the **regio olfactoria**, which embraces the upper part of the septum, the upper turbinated bone and part of the middle (*Cm*) turbinated bone (fig. 738, *Cs*). All the remainder of the nasal cavity is called the **regio respiratoria**. These two regions are distinguished as follows:—(1) The regio olfactoria has a thicker mucous membrane. (2) It is covered by a single layer of cylindrical epithelium, the cells being often branched at their lower ends, and contain a yellow or brownish-red pigment (figs. 739, 740, E). (3) It is coloured by this pigment, and is thereby distinguished from the uncoloured regio respiratoria, which is covered by ciliated epithelium. (4) It contains peculiar tubular glands (**Bowman's glands**), described as "mixed glands" by Paulsen (§ 142), while the rest of the mucous membrane contains numerous acinous *serous* glands (*Heidenhain*); but in man the latter are said to be mixed glands (*Stöhr*) (fig. 739). Lymph-follicles lie in the mucous membrane, and from them numerous leucocytes pass on to the free surface (*Stöhr*). (5) Lastly, the regio olfactoria embraces the end-organs of the olfactory nerve. The long narrow **olfactory cells**

(fig. 740, N) are distributed between the ordinary cylindrical epithelium (E) covering the regio olfactoria. The body of the cell is spindle-shaped, with a large nucleus

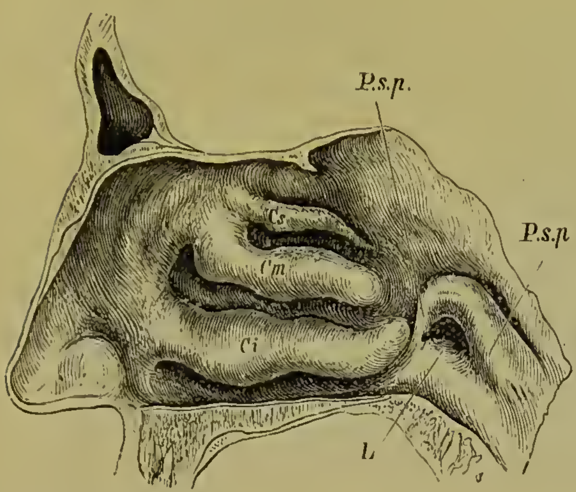


Fig. 738.

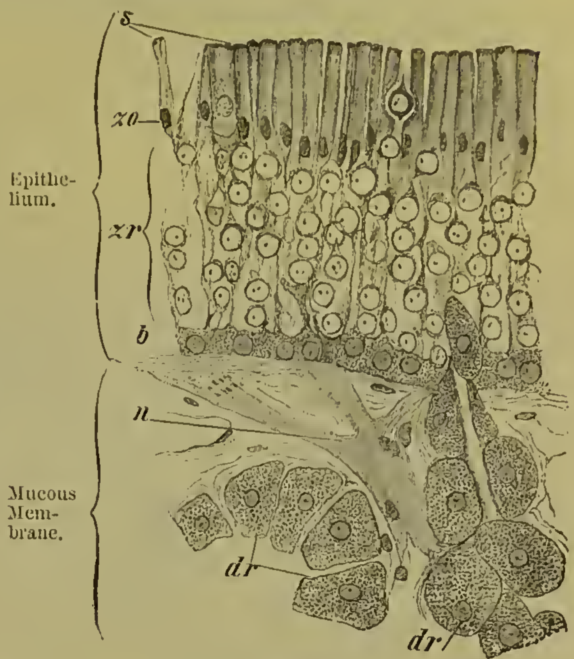


Fig. 739.

Fig. 738.—Nasal and pharyngo-nasal cavities. *L*, levator elevation; *P.s.p.*, plica salpingo-palatina; *Cs*, *Cm*, *Ci*, the three turbinated bones. Fig. 739.—Vertical section of the olfactory region (rabbit), × 560. *s*, disc; *zo*, zone of oval, and *zr* of spherical nuclei; *b*, basal cells; *dr*, part of a Bowman's gland; *n*, branch of the olfactory nerve.

containing nucleoli, and it sends upwards between the cylindrical cells a narrow (0·9 to 1·8 μ) smooth rod, quite up to the free surface of the mucous membrane. In the frog (*n*) the free end carries delicate projecting hairs or bristles. In the deeper part of the mucous membrane, the olfactory cells pass into, and become continuous with, varicose fine nerve-fibres, which pass into the olfactory nerve (§ 321, I., 1). According to C. K. Hoffman and Exner, after section of the olfactory nerve, the specific olfactory end-organs become changed into cylindrical epithelium (frog), and in warm-blooded animals they undergo fatty degeneration, even on the 15th day. V. Brunn found a homogeneous limiting membrane, which had holes in it for transmitting the processes of the olfactory cells only.

[The **respiratory part** of the nasal mucous membrane is lined by **ciliated** epithelium stratified like that in the trachea and resting on a basement membrane. Below this there are many lymph-corpuscles and aggregations of adenoid tissue.]

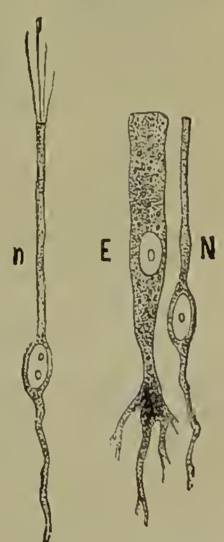


Fig. 740.

N, olfactory cells (human); *n*, from the frog; E, epithelium of the regio olfactoria.

[The **organ of Jacobson** is present in all mammals, and consists of two narrow tubes protected by cartilage, and placed in the lower and anterior part of the nasal septum. Each tube terminates blindly behind, but anteriorly it opens into the nasal furrow or into the naso-palatine canal (dog). The wall next the middle line is covered by olfactory epithelium, and receives olfactory nerves (rabbit, guinea-pig), and it contains glands similar to those of the olfactory region; the outer wall is covered by columnar epithelium ciliated in some animals (*Klein*).]

[The olfactory non-medullated nerves arise from the **olfactory bulb**, which is

a greyish-yellow small rounded mass lying on the orbital surface of the frontal lobe and upon the cribriform plate of the ethmoid bone (fig. 741). It is connected to the brain behind by the **tractus olfactorius**, which is triangular in cross-section and runs backwards to the substantia perforata anterior. Its roots have been described already (§ 343, I.), but some of its fibres can be traced into the uncinate gyrus of the temporal lobe to the nucleus amygdaleus and cornu ammonis, while some fibres cross to the opposite side at the anterior border of the anterior commissure.]

[The olfactory tract and bulb were originally a protrusion of the cerebral substance, and contained within them a narrow cavity continuous with the middle cornu of the lateral ventricle. Both the bulb and tract contain grey and white matter, and in the former are many corpora amylacea.]

[In a sagittal section of the tract and bulb in the dog (fig. 742) we see that the bulb (*b*) covers the tract (*t*) like a hood, while in the interior is seen the narrow canal. The olfactory tract is triangular in cross-section with rounded edges and slightly concave sides. At

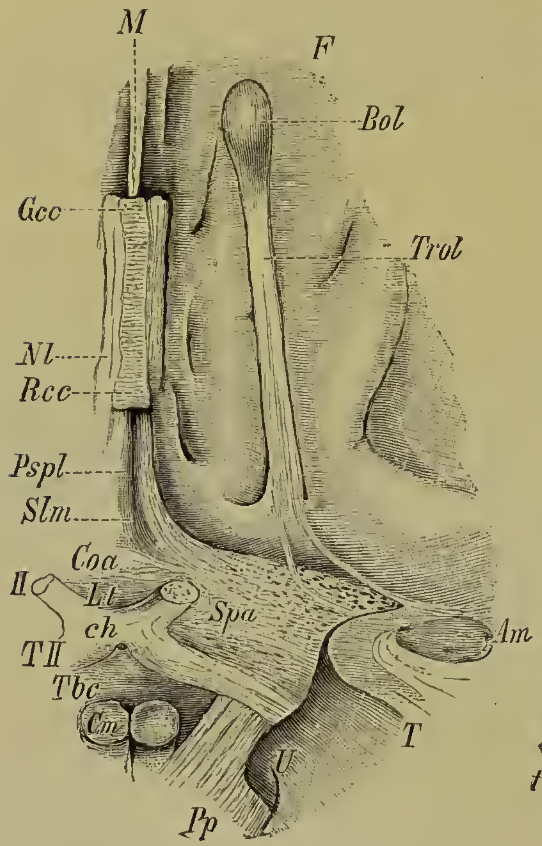


Fig. 741.

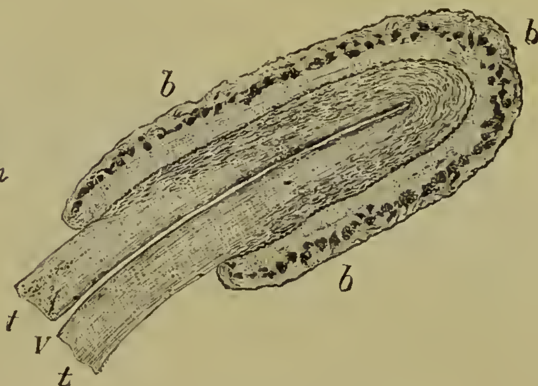


Fig. 742.

Fig. 741.—Part of the base of the brain showing the *Pp*, pes pedunculi; *Cm*, corpus mammillare; *Tbc*, tuber cinereum; T II, and II, optic tract and nerve; *ch*, chiasma; *T*, temporal lobe; *U*, uncus; *Am*, nucleus amygdaleus; *Spa*, anterior perforated spot; *Lt*, lamina terminalis; *Coa*, position of anterior commissure; *F*, frontal lobe; *Bol*, olfactory bulb; *Trol*, olfactory tract. Fig. 742.—Sagittal section of the olfactory bulb of a dog; *b*, olfactory bulb; *t*, olfactory tract; *v*, ventricle of the bulb. × 4.

its basal part and covering the lateral angles are numerous fine medullated fibres, and there are also medullated nerve-fibres on its dorsal aspect. The more central parts of the tract contain connective-tissue and some small nerve-cells.]

[The **olfactory bulb** consists of many layers as seen on vertical section. Most superficially it is covered by a layer of pia mater, and under it are numerous bundles of the fibres of the olfactory nerve—the *nerve-fibre layer* (fig. 743, D). The second layer, *stratum glomerulosum* (fig. 743, E), contains peculiar globular masses, closely packed together, and passing into them are nerve-fibres from the first layer. In these glomeruli the nerve-fibrils come into relation with fibrils, the branches of nerve-cells. The third layer is the *stratum gelatinosum* (fig. 743), consisting of a finely granular ground-substance in which are scattered some branched cells, and through it there pass branches of nerve-fibres and nerve-cells. The fourth or *nerve-cell layer* (fig. 743, C) consists partly of a single layer of large branched

nerve-cells which give off an axis-cylinder process centrally and protoplasmic processes peripherally. The latter enter the glomeruli. The next layer—*stratum granulosum*—consists of bundles of nerve-fibres with numerous granules intercalated amongst them. The innermost or sixth layer contains medullated nerve-fibres. The similarity between the elements contained in the olfactory bulb and those in the retina has been pointed out by many observers.]

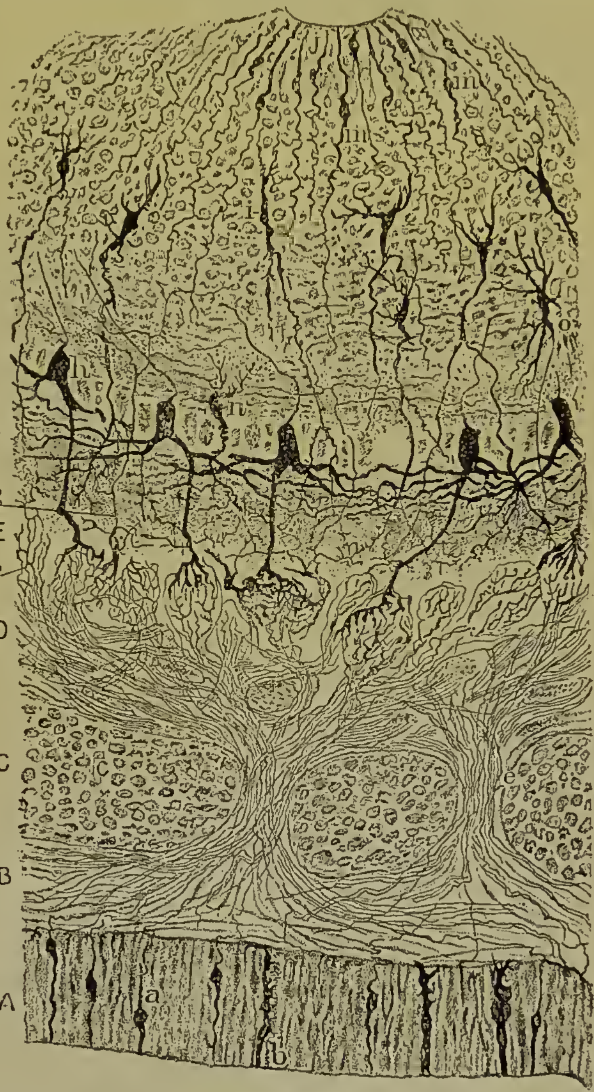


Fig. 743.

Antero-posterior section of the olfactory bulb and nasal mucous membrane of a new-born mouse. A, olfactory epithelium situated below the lamina cribrosa; *a*, bipolar cells, and *b*, sustentacular cells. B, substantia propria of the mucosa with numerous nerve-fibres. C, ethmoidal cartilage; D, layer of olfactory nerve-fibres; E, layer of olfactory glomeruli; F, inferior molecular layer; G, layer of multipolar nerve-cells; H, superior molecular layer; I, granular layer; *c*, cartilage; *e*, olfactory nerves; *f*, ramifications of the olfactory fibrils in the glomeruli; *g*, central axis-cylinder process of a cell; *h*, multipolar nerve-cell; *i*, granules; *j*, epithelial cells; *m*, terminal filament of an epithelial cell; *o*, large cell (*Cayal*).

421. OLFACTORY SENSATIONS.—Olfactory sensations are produced by the action of gaseous, odorous substances being brought into **direct contact** with the olfactory cells during the act of *inspiration*. The current of air is divided by the anterior projection of the lowest turbinated bone, so that a part above the latter is conducted to the regio olfactoria. During inspiration, the air streams along close to the septum, while little of it passes through the nasal passages, especially the superior (*Paulsen and Exner*). [The expired air takes almost the same course as the inspired air.] Odorous bodies taken into the mouth and then expired through the posterior nares are said not to be smelt (*Bidder*). [This is certainly not true, as has been proved by Aronsohn.]

[It is usually stated that only odorous particles suspended in air excite the sensation of smell. This is certainly not the whole truth—otherwise, how do aquatic animals, like fish, smell? Moreover the mucous membrane is always moist, and in some cases where there is a profuse secretion from the olfactory mucous membrane, there is no impairment of the sense of smell.]

The *first* moment of contact between the odorous body and the olfactory mucous membrane appears to be the time when the sensation takes place, as, when we wish to obtain a more exact perception, we *sniff* several times, *i.e.*, a series of rapid inspirations are taken, the mouth being kept closed. During **sniffing**, the air within the nasal

cavities is rarefied, and as air rushes in to equilibrate the pressure, the air, laden with odorous particles, streams over the olfactory region. Odorous fluids are said not to give rise to the sensation of smell when they are brought into direct contact with the olfactory mucous membrane, as by pouring eau de Cologne into the nostrils (*Tourtual*, 1827; *E. H. Weber*, 1847). [Aronsohn has, however, shown that these experiments are not accurate, for one can smell eau de Cologne, clove oil, &c., when a mixture of these bodies with ·75 per cent. NaCl is applied to the olfactory mucous membrane; the most suitable medium is ·73 per cent. NaCl and its temperature 40–43° C.] Even water alone temporarily affects the cells. We know practically nothing about the nature of the action of odorous bodies, but many odorous vapours have a considerable power of absorbing heat (*Tyndall*). [Odorous bodies diminish the number of respirations (*Gourewitsch*).]

The **intensity of the sensation** depends on—**1.** The size of the olfactory surface, as animals with a very keen sense of smell are found to have complex turbinated bones covered by the olfactory mucous membrane. **2.** The concentration of the odorous mixture of the air. Still, some substances may be attenuated enormously (*e.g.*, musk to the two-millionth of a milligram), and still be smelt. **3.** The frequency of the conduction of the vapour to the olfactory cells (sniffing).

[The **acuteness** of the sense of smell is greatly improved by practice. A boy named James Mitchell, who was deaf, dumb, and blind, used his sense of smell, like a dog, to distinguish persons and things.]

[As in the case of sight and hearing, it has been sought to connect the *quality* of taste and smell with the *kind* of vibrating stimulus. Ramsay showed that many facts pointed to the dependence of smell upon the vibratory motion of odorous particles; thus, many gases and vapours of low specific gravity—*i.e.*, with a very rapid vibration of their molecules—are perfectly odourless, while such substances as the alcohols and fatty acids, alike in chemical and physical properties, can excite generic smells, the higher members of the group being more powerful in this respect than the lower ones. Taking the elements as arranged in a "Natural Classification" by Mendelejeff, Haycraft has shown that elements in the same group are capable of producing similar or related tastes, and the same seems to be true for smell (*Haycraft*).]

We can smell the following substances in the following proportions: Bromine $\frac{1}{30000}$, sulphuretted hydrogen $\frac{1}{5000000}$ milligram in 1 c.cm. of air (*Valentin*); also $\frac{1}{4600000}$ of a milligram of chlorphenol, and $\frac{1}{4600000000}$ of a milligram of mercaptan (*E. Fischer and Penzoldt*).

[Althaus found that **electrical stimulation** of the olfactory mucous membrane gave rise to the sensation of the smell of phosphorus, and Aronsohn found that he smelt on making the current when the cathode—and on breaking the current when the anode—was in the nose.]

The **variations** are referred to in § 343. If the two nostrils are filled with different odorous substances there is no mixture of the odours, but we smell sometimes the one and sometimes the other (*Valentin*). [Some substances appear to affect some regions of the olfactory membrane, while others affect other parts.] The sense of smell, however, is very soon blunted, or even paralysed. [It can be blunted or fatigued in a few minutes; but after it is completely fatigued it can recover in a minute.] Morphia, when mixed with a little sugar and taken as snuff, paralyses the olfactory apparatus, while strychnin makes it more sensitive (*Lichtenfels and Fröhlich*).

The **sensory** nerves of the nasal mucous membrane (§ 347, II.) [*i.e.*, those supplied from the fifth cranial nerve] are stimulated by irritating vapours, and may even cause pain, *e.g.*, ammonia and acetic acid. In a very diluted condition they may even act on the olfactory nerves. The nose is useful as a sentinel for guarding against the introduction of disagreeable odours and foods. The sense of smell is aided by the sense of taste, and conversely.

[**Flavour** depends on the sense of smell, and, to test it, use substances, solid or fluid, with an *aroma* or *bouquet*, such as wine or roast beef.]

[**Method of Testing.**—In doing so, avoid the use of pungent substances like ammonia, which excite the fifth nerve. Use some of the essential volatile oils, such as cloves, bergamot, and the fœtid gum resins, or musk and camphor. Electrical stimuli are not suitable. **Action of Drugs**, § 343.]

Comparative.—In the lowest **vertebrata**, pits, or depressions provided with an olfactory nerve, represent the simplest olfactory organ. Amphioxus and the cyclostomata have only *one*

olfactory pit ; all other vertebrates have two. In some animals (frog) the nose communicates with the mouth by ducts. The olfactory nerve is absent in the whale.

Historical.—Rufus Ephesius (97 A.D.) described the passage of the olfactory nerve through the ethmoid bone. Rudius (1600) dissected the body of a man with congenital anosmia, in whom the olfactory nerves were absent. Magendie originally supposed that the nasal branch of the fifth was the nerve of smell, a view successfully combated by Eschricht.

The Sense of Taste.

422. **STRUCTURE OF THE GUSTATORY ORGANS.—Gustatory Region.**—There is considerable difference of opinion as to what regions of the mouth are endowed with taste :—(1) The root of the tongue in the neighbourhood of the circumvallate papillæ, the area of distribution of the glosso-pharyngeal nerve, is undoubtedly endowed with taste (§ 351). The filiform papillæ and about 20 per cent. of the fungiform do not administer to taste (*Oehrwall*). (2) The tip and margins of the tongue are gustatory by means of the fungiform papillæ, but

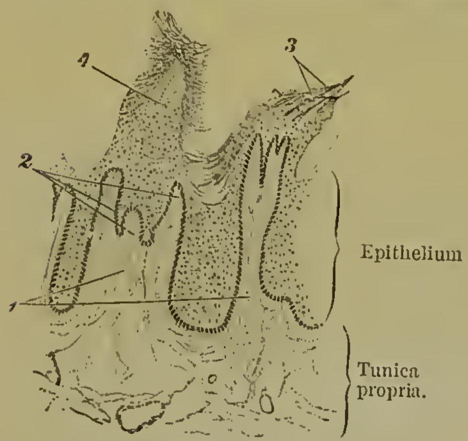


Fig. 744.

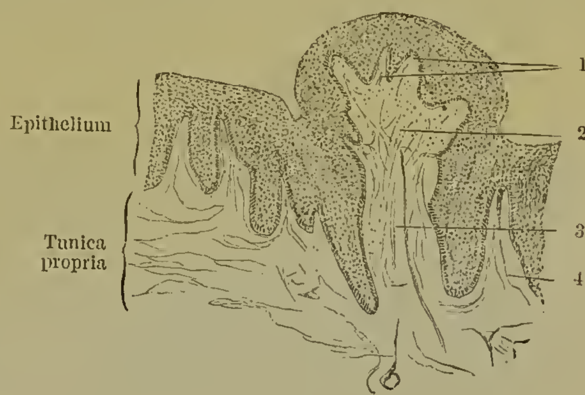


Fig. 745.

Fig. 744.—Longitudinal section of the dorsum of the human tongue. 1, section of two filiform papillæ, with secondary papillæ (2) ; 3, double, 4, single process of epithelium with loose epithelial scales. × 30. Fig. 745.—Longitudinal section of the human tongue. 1, secondary papillæ on 2, the fungiform papilla ; 3, base of 2 ; 4, small filiform papilla. × 30.

there are very considerable variations. (3) The lateral part of the soft palate and the glosso-palatine arch are endowed with taste from the glosso-pharyngeal nerve. (4) It is uncertain whether the hard palate and the entrance to the larynx are endowed with taste (*Drielsma*). The middle of the tongue is not gustatory.

[**Tongue—Mucous membrane.**—The structure of the tongue, as a muscular organ covered with mucous membrane, has already been described (§ 155). The dorsal surface of the tongue, in front of the blind foramen, is beset with elevations of the mucous membrane, which extend to its tip and borders. These elevations, or **papillæ**, are of three kinds :—**filiform**, **fungiform**, and **circumvallate**. They consist of elevations of the mucous membrane, visible to the naked eye, and covered by stratified squamous epithelium, while the central core of connective-tissue contains blood- and lymph-vessels and nerves. The **filiform papillæ** occur over the whole tongue, and are smallest and most numerous. They are conical eminences, covered by stratified squamous epithelium, and often beset with secondary papillæ (fig. 744). The **fungiform papillæ** occur chiefly

over the middle and front part of the tongue, and are not so numerous as the last. They are club-shaped, with a narrow base, and broad expanded rounded head. They also have secondary papillæ. They are generally brighter red than the others (fig. 745). The **circumvallate papillæ**, 8 to 12 in number, diverge from the foramen cæcum at the back part of the tongue in two rows in the form of a wide V, the open angle of the V being directed forwards. They are large, with a broad expanded top, and are lodged in a depression of the mucous membrane, being surrounded by a wall of mucous membrane, and separated from it by a circular trench, into the base of which gland-ducts often open. They have numerous secondary papillæ, and in them are taste-buds, fig. 746, I.]

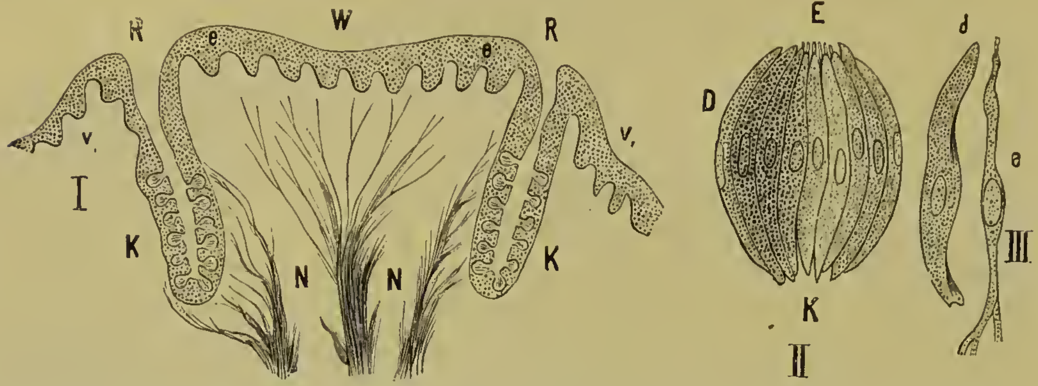


Fig. 746.

I. Transverse section of a circumvallate papilla; W, the papilla; v_1, v_1, the wall in section, R, R, the circular slit or fossa; K, K, the taste-bulbs in position; N, N, the nerves. II. Isolated taste-bulb; D, supporting or protective cells; K, lower end; E, free end, open, with the projecting apices of the taste-cells. III. Isolated protective cell (*d*) with a taste cell (*e*).

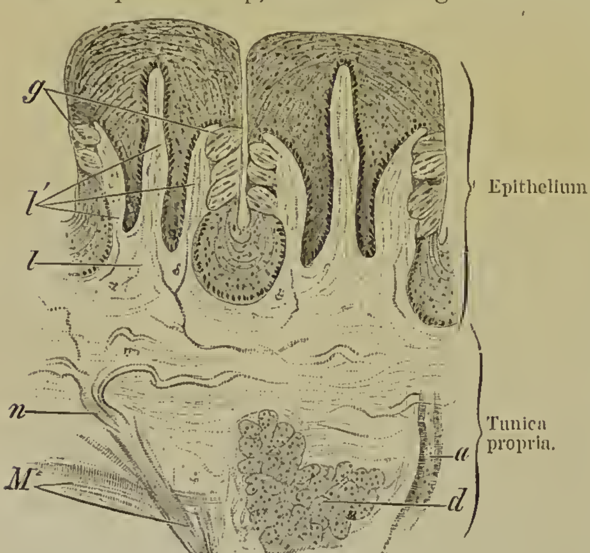


Fig. 747.

Vertical section of two septa of the papilla foliata (rabbit). ×80. Each septum, *l*, has secondary septa, *l'*; *g*, taste-buds; *n*, medullated nerve; *d*, serous gland, and part of its duct, *a*; *M*, muscular fibres of the tongue.

Taste-bulbs.—The **end-organs** of the gustatory nerves are the taste-bulbs or taste-buds discovered by Schwalbe and Lovèn (1867). They occur on the lateral surfaces of the circumvallate papillæ (fig. 746, I), and upon the opposite side, K, of the fossa or capillary slit, R, R, which surrounds the central eminence or papilla; they occur more rarely on the surface. They also occur in the fungiform papillæ, in the papillæ of the soft palate and uvula (*A. Hoffmann*), on the under surface of the epiglottis, the upper part of the posterior surface of the epiglottis, and the inner side of the arytenoid cartilages (*Verson, Davis*), and on the vocal cords (*Simanowsky*). Many buds or bulbs disappear in old age.

[In the rabbit and some other animals, there is a folded laminated organ on each

side of the posterior part of the tongue, called the **papilla foliata**; the folds have on each side of them numerous taste-buds (fig. 746).]

Structure of the taste-bulbs.—They are 81 μ high and 33 μ thick, barrel-shaped, and embedded in the thick stratified squamous epithelium of the tongue. Each bulb consists of a series of lancet-shaped, bent, nucleated, outer **supporting** or **protective cells**, arranged like the staves of a barrel (fig. 746, II, D, isolated in III, *a*). They are so arranged as to leave a small opening, or the "**gustatory pore**," at the free end of the bulb. Surrounded by these cells, and lying in the axis of the bud, are 1 to 10 **gustatory cells** (II, E), some of which are provided with a delicate process (III, *e*) at their free ends while their lower fixed ends send out basal processes, which becomes continuous with the terminations of the nerves of taste, which have become non-medullated. After section of the glosso-pharyngeal nerve, the taste-buds degenerate, while the protective cells become changed into ordinary epithelial cells within four months (*v. Vintschgau and Hönigschmied*). Very similar structures were found by Leydig in the skin of fresh-water fishes. The *glands* of the tongue and their secretory fibres from the 9th cranial nerve are referred to in § 141 (*Drasch*).

423. GUSTATORY SENSATIONS.—Varieties.—There are *four* different gustatory qualities, the sensations of—

1. **Sweet.**	3. **Acid.**
2. **Bitter.**	4. **Saline.**

Acid and saline substances at the same time also stimulate the sensory nerves of the tongue, but when greatly diluted, they only excite the end-organs of the specific nerves of taste. Perhaps there are special nerve-fibres for each different gustatory quality (*v. Vintschgau*).

Conditions.—Sapid substanees, in order that they may be tasted, require the following conditions:—They must be **dissolved** in the fluid of the mouth, especially substances that are solid or gaseous. The **intensity** of the gustatory sensation depends on:—**1.** The *size of the surface* acted on. Sensation is favoured by rubbing in the substance between the papillæ; in fact, this is illustrated in the rubbing movements of the tongue during mastication (§ 354). **2.** The *concentration* of the sapid substance is of great importance. Valentin found that the following series of substances ceased to be tasted in the order here stated, as they were gradually diluted—syrup, sugar, common salt, aloes, quinine, sulphuric acid. Quinine can be diluted 20 times more than common salt and still be tasted (*Camerer*). **3.** The *time* which elapses between the application of the sapid substance and the production of the sensation varies with different substances. Saline substances are tasted most rapidly (after 0·17 second, according to *v. Vintschgau*), then sweet, acid, and bitter (quinine after 0·258 second, *v. Vintschgau*). This even occurs with a mixture of these substances (*Schirmer*). The last-named substances produce the most persistent "**after-taste.**" **4.** The *delicacy* of the sense of taste is partly congenital, but it can be greatly improved by practice. If a person continues to taste the same sapid substance, or a nearly related one, or even any very intensely sapid substance, the gustatory sense is soon affeeted, and it beeomes impossible to give a correct judgment as to the taste of the sapid body. **5.** Taste is greatly aided by the sense of **smell**, and in fact we often confound taste with smell; thus, ether, chloroform, musk, and assafœtida only affect the organ of smell. [The combined action of taste and smell in some cases gives rise to **flavour** (p. 1008).] The eye even may aid the determination, as in the experiment where in rapidly tasting red and white wine one after the other, when the eyes are covered, we soon become unable to distinguish between the one and the other. **6.** The most advantageous *temperature* for taste is between 10° to 35° C.; hot and cold water temporarily paralyse taste.

[Oehrwall and others, by applying to the back of the tongue different solutions by means of a fine brush, found that certain filiform papillæ reacted only to sugar, and not to tartaric acid, some which reacted to the application of quinine, but not to tartaric acid, and others which reacted to quinine, but not to sugar. By means of electrical stimulation bitter, saline, or sweet tastes could be produced. With the constant current the purest sensation occurred at the anode.]

[The peculiar "**metallic taste**" which accompanies diffuse electrical stimulation of the gustatory mucous membrane is a mixed sensation due to bitter, saline, and sensory impressions. Continued stimulation excites fatigue of certain tastes. These results may be explained by supposing that there are **specific end-organs** administering to the several varieties of taste, and which are distributed in different proportions in the different papillæ.]

Ice placed on the tongue suppresses, sometimes entirely, the whole gustatory apparatus; cocain alone, bitter tastes, and water containing 2 per cent. of H_2SO_4, excite afterwards a sweet taste (*Aducco and Mosso*).

Electrical Current.—The **constant current**, when applied to the tongue, excites, both during its passage and when it is opened or closed, a sensation of acidity at the + pole, and at the − pole an alkaline taste, or, more correctly, a harsh burning sensation (*Sulzer*, 1752). This is not due to the action of the electrolytes of the fluid in the mouth, for even when the tongue is moistened with an acid fluid the alkaline sensation is experienced at the − pole (*Volta*). We cannot, however, set aside the supposition that perhaps electrolytes, or decomposition-products, may be formed in the deeper parts and excite the gustatory fibres. Rapidly **interrupted currents** do not excite taste (*Grünhagen*). V. Vintschgau, who has only incomplete taste on the tip of the tongue, finds that when the *tip* of the tongue is traversed by an electrical current, there is never a gustatory sensation, but always a distinct tactile one. In experiments on Hönigschmied, who is possessed of normal taste in the tip of the tongue, there was often a metallic or acid taste at the + pole on the tip of the tongue, while at the − pole taste was often absent, and when it was present it was almost always alkaline, and acid only exceptionally. After interrupting the current there was a **metallic after-taste** with both directions of the current.

[**Testing Taste.**—Direct the person to put out his tongue and close his eyes, and after drying the tongue apply the sapid substance by means of a glass rod or a small brush. Try to confine the stimulus as much as possible to one place, and after each experiment rinse the mouth with water. A wine-taster chews an olive to "clean the palate," as he says. For testing *bitter* taste use a solution of quinine or quassia; for *sweet*, sugar [or the intensely sweet substance "saccharine" obtained from coal tar]; *saline*, common salt; and *acid*, dilute citric or acetic acid. The galvanic current may also be used.]

Pathological.—Diseases of the tongue, as well as dryness of the mouth caused by interference with the salivary secretion, interfere with the sense of taste. **Subjective gustatory** impressions are common amongst the insane, and are due to some central cause, perhaps to irritation of the centre for taste (§ 378, IV., 3). After poisoning with santonin, a bitter taste is experienced, while after the subcutaneous injection of morphia, there is a bitter and acid taste. The terms **hypergeusia**, **hypogeusia**, and **ageusia** are applied to the increase, diminution, and abolition of the sense of taste. Many tactile impressions on the tongue are frequently confounded with gustatory sensations, *e.g.*, the so-called biting, cooling, prickling, sandy, mealy, astringent, and harsh tastes.

Comparative.—About 1760 taste-bulbs occur on the circumvallate papillæ of the ox. The term **papilla foliata** is applied to a large folded gustatory organ placed laterally on the side of the tongue (fig. 747), especially of the rabbit (*Rapp*, 1832), which in man is represented by analogous organs, composed of longitudinal folds, lying in the fimbriæ linguæ on each side of the posterior part of the tongue (*Krause, v. Wyss*). Taste-bulbs are absent in reptiles and birds. They are numerous in the gill-slits of the tadpole (*F. E. Schultze*), while the tongue of the frog is covered with epithelium resembling gustatory cells (*Billroth, Axel Key*). The goblet-shaped organs in the skin of fishes and tadpoles have a structure similar to the taste-bulbs, and may perhaps have the same function. There are taste-bulbs in the mouth of the carp and ray.

Historical.—Bellini regarded the papillæ as the organs of taste (1711). Richerand, Mayo, and Fodera thought that the lingual was the only nerve of taste, but Magendie proved that, after it was divided, the posterior part of the tongue was still endowed with taste. Panizza (1834) described the glosso-pharyngeal as the nerve of taste, the gustatory as the nerve of touch, and the hypoglossal as the motor nerve of the tongue.

The Sense of Touch.

424. TERMINATIONS OF SENSORY NERVES.—1. The **touch-corpuscles of Wagner and Meissner** lie in the **papillæ** of the cutis vera (§ 283), and are most numerous in the palm of the hand and the sole of the foot, especially in the fingers and toes, there being about 21 to every square millimetre of skin, or 108 to 400 of the papillæ containing blood-vessels. They are less abundant on the back of the hand and foot, mamma, lips, and tip of the tongue, rare on the glans clitoridis, and occur singly and scattered on the volar side of the fore-arm, even in the anthropoid apes. They are oval or elliptical bodies, 40–200 μ long [$\frac{1}{300}$ in.], and 60–70 μ broad [$\frac{1}{300}$ to $\frac{1}{500}$ in.], and are covered externally by layers of connective-tissue arranged trans-

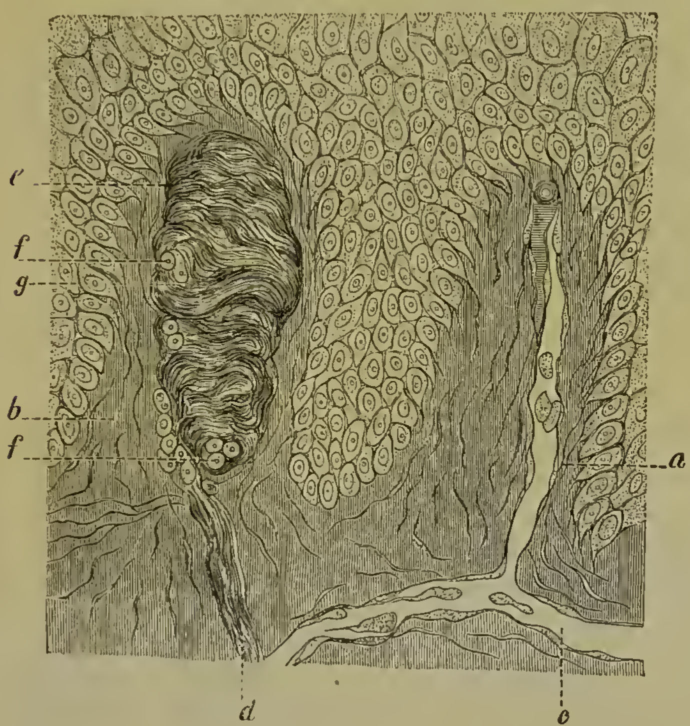


Fig. 748.

Fig. 749.

Fig. 748.—Vertical section of the skin of the palm of the hand. *a*, blood-vessels ; *b*, papilla of the cutis vera ; *c*, capillary ; *d*, nerve-fibre passing to a touch-corpuscle ; *f*, nerve-fibre divided transversely ; *e*, Wagner's touch-corpuscle ; *g*, cells of the Malpighian layer of the skin. Fig. 749.—Wagner's touch-corpuscle from the palm, treated with gold chloride ; *n*, nerve-fibres ; *a*, *a*, groups of glomeruli.

versely in layers, and within is a granular mass with elongated striped nuclei (figs. 748, 749, *e*). One to three medullated nerve-fibres pass to the lower end of each corpuscle, and surround it in a spiral manner two or three times; the fibres then lose their myelin, and, after dividing into 4 to 6 fibrils, branch within the corpuscle. The exact mode of termination of the fibrils is not known. Some observers suppose that the transverse fibrillation is due to the coils or windings of the nerve-fibrils ; while according to others, the inner part consists of numerous flattened cells lying one over the other, between which the pale terminal fibres end either in swellings or with disc-like expansions, such as occur in Merkel's corpuscles.

[These do not contain a soft core such as exists in Pacini's corpuscles. The corpuscles appear to consist of connective-tissue with imperfect septa passing into the interior from the fibrous

capsule. After the nerve-fibre enters it loses its myelin, and then branches, while the branches anastomose and follow a spiral course within the corpuscle, finally to terminate at slight enlargements. According to Thin, there are simple and compound corpuscles, depending on the number of nerve-fibres entering them.]

Kollmann describes three special tactile areas in the hand :—(1) The tips of the fingers with 24 touch-corpuscles in a length of 10 mm. ; (2) the three eminences lying on the palm behind the slits between the fingers, with 5·4–2·7 touch-corpuscles in the same length ; and (3) the ball of the thumb and little finger with 3·1–3·5 touch-corpuscles. The first two areas also contain many of the corpuscles of Vater or Pacini, while in the latter these corpuscles are fewer and scattered. In the other parts of the hand the nervous end-organs are much less developed.

2. **Vater's (1741) or Pacini's corpuscles** are oval bodies (fig. 750), 1–2 mm. long, lying in the subcutaneous tissue on the nerves of the fingers and toes (600–1400), in the neighbourhood of joints and muscles, the sympathetic abdominal plexuses, near the aorta and coccygeal gland, on the dorsum of the penis and clitoris, and in the mesocolon [and mesentery] of the cat. [They also occur in the course of the intercostal and periosteal nerves, and Stirling has seen them in the capsule of lymphatic glands. They are attached to the nerves of the hand and feet, and are so large as to be visible to the naked eye, both in these regions and between the layers of the mesentery of the cat. They are whitish or somewhat transparent, with a white line in the centre (cat) ; in man, they are $\frac{1}{15}$ to $\frac{1}{10}$ inch long, and $\frac{1}{25}$ to $\frac{1}{20}$ inch broad, and are attached by a stalk or pedicle (fig. 750, *a*) to the nerve.] They consist of numerous nucleated connective-tissue capsules or **lamellæ** lined by endothelium, separated from

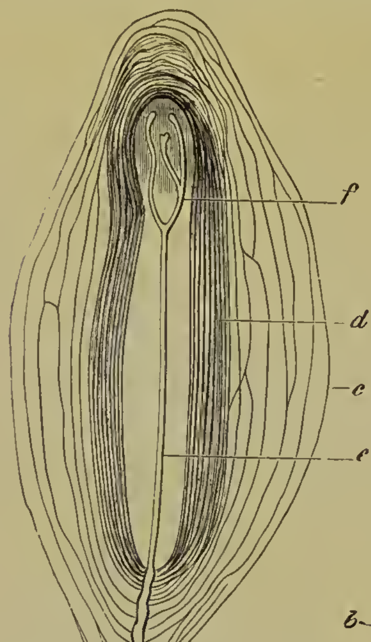


Fig. 750.

Fig. 751.

Fig. 752.

Fig. 750.—Vater's or Pacini's corpuscle. *a*, stalk ; *b*, nerve-fibre entering it ; *c*, *d*, connective-tissue envelope ; *e*, axis-cylinder, with its end divided at *f*. Fig. 751.—End-bulb from human conjunctiva. *a*, nucleated capsule ; *b*, core ; *c*, fibre entering and branching, terminating in core at *d*. Fig. 752.—Tactile corpuscles (clitoris of rabbit).

each other by fluid, and lying one within the other like the coats of an onion, while in the axis is a **central core**. A medullated nerve-fibre passes to each, where its sheath of Schwann unites with the capsule. It loses its myelin, and passes into the interior as an axial cylinder (fig. 750, *e*), where it either ends in a small knob or may divide dichotomously (fig. 750, *f*), each branch terminating in a small pear-shaped *enlargement*. [Each large corpuscle is covered by 40–50 **lamellæ**, or tunics,

which are thinner and closer to each other (fig. 750, *d*) internally than in the outer part, where they are thicker and wider apart. The lamellæ are like the laminæ in the lamellated sheath of a nerve, and are composed of an elastic basis mixed with white fibres of connective-tissue, while the inner surface of each lamellæ is lined by a single continuous layer of endothelium continuous with that of the perineurium. It is easily stained with silver nitrate. The **efferent nerve-fibre** is covered with a thick sheath of lamellated connective-tissue (sheath of Henle), which becomes blended with the outer lamellæ of the corpuscle. The medullated nerve is sometimes accompanied by a blood-vessel, and pierces the various tunics, retaining its myelin until it reaches the core, where it terminates as already described.]

3. **Krause's end-bulbs** very probably occur as a regular mode of nerve-termination in the cutis and mucous membranes of all mammals (fig. 751). They are elongated, oval, or round bodies, 0·075 to 0·14 mm. long, and have been found in the deeper layers of the conjunctiva bulbi, floor of the mouth, margins of the lips, nasal mucous membrane, epiglottis, fungiform and circumvallate papillæ, glans penis and clitoris, volar surface of the toes of the guinea-pig, ear and body of the mouse, and in the wing of the bat. [In the calf the "**cylindrical end-bulbs**" are oval, with a nerve-fibre terminating within them. The sheath of Henle becomes continuous with the nucleated capsule, while the axial cylinder, devoid of its myelin, is continued into the soft core. In man the end-bulbs are "spheroidal," and consist of a nucleated connective-tissue capsule continuous with Henle's sheath of the nerve, and enclosing many cells, amongst which the axis-cylinder which enters the bulb branches and terminates.] The spheroidal end-bulbs occur in man, in the nasal mucous membrane, conjunctiva, mouth, epiglottis, and the mucous folds of the rectum. According to Waldeyer and Longworth, the nerve-fibrils terminate in the cells within the capsule. These cells are said to be comparable to Merkel's tactile cells (*Waldeyer*).

Fig. 753.
Vertical section of the epithelium of the cornea nerve-endings in the cornea.

The **genital corpuscles** of Krause, which occur in the skin and mucous membrane of the glans penis, clitoris, and vagina, appear to be end-bulbs more or less fused together (fig. 752).

The **articulation nerve-corpuscles** occur in the synovial mucous membrane of the joints of the fingers. They are larger than the end-bulbs, and have numerous oval nuclei externally, while one to four nerve-fibres enter them.

4. **Tactile** or **touch-corpuscles of Merkel**, sometimes also called the **corpuscles of Grandry**, occur in the beak and tongue of the duck and goose, in the epidermis of man and mammals, and in the outer root-sheath of tactile hairs or feelers (fig. 754). They are small bodies composed of a capsule enclosing two, three, or more large, granular, somewhat flattened nucleated and nucleolated cells, piled one on the other in a vertical row like a row of cheeses. Each corpuscle receives at one side a medullated nerve-fibre, which loses its myelin, and branches, to terminate, according to some observers (*Merkel*), in the cells themselves, and according to others (*Ranvier*, *Izquierdo*, *Hesse*) in the protoplasmic transparent substance or disc lying between the cells. [This intercellular disc is the "**disc tactil**" of Ranvier, or the "*Tastplatte*" of Hesse.] When there is a great aggregation of these cells, large structures are formed, which appear to form a kind of transition between these and touch-corpuscles. [According to Klein, the terminal fibrils end neither in the touch-cells nor tactile disc, but in minute swellings in

the interstitial substance between the touch-cells, in a manner very similar to that occurring in the end-bulbs.]

[According to Merkel, tactile cells, either isolated or in groups, but in the latter case never forming an independent end-organ, occur in the deeper layers of the epidermis of man and mammals and also in the papillæ. They consist of round or flask-shaped cells, with the lower pointed neck of the flask continuous with the axis-cylinder of a nerve-fibre. They are regarded by Merkel as the simplest form of a tactile end-organ, but their existence is doubted by some observers.]

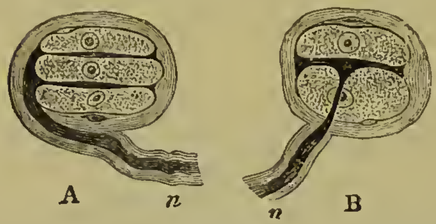


Fig. 754.

Fig. 755.

Fig. 754.—Tactile corpuscles from the duck's tongue. A, composed of three cells with two interposed discs, with axis-cylinder, *n*, passing into them. B, two tactile cells and one disc. Fig. 755.—Bouchon epidermique from the nose of a guinea-pig, after the action of gold chloride. *n*, nerve-fibre ; *a*, tactile cells ; *m*, tactile discs ; *c*, epithelial cells.

Amongst animals there are many other forms of sensory end-organs. [**Herbst's corpuscles** occur in the mucous membrane of the tongue of the duck, and resemble small Vater's corpuscles, but their lamellæ are thinner and nearer each other, while the axis-cylinder within the central core is bordered on each side by a row of nuclei.] In the nose of the mole there is a peculiar end-organ (*Eimer*), while there are "*end-capsules*" in the penis of the hedgehog and the tongue of the elephant, and "*nerve-rings*" in the ears of the mouse.

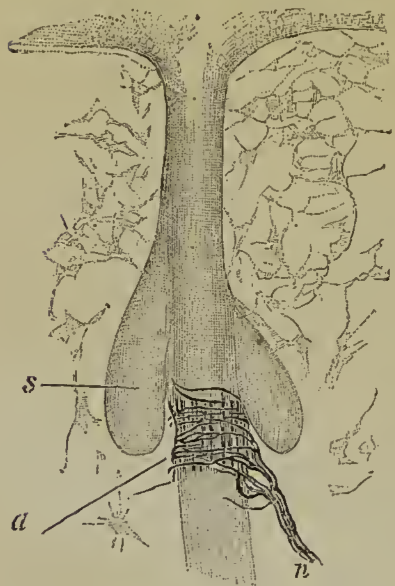


Fig. 756.

Termination of nerve-fibres, (*a*) in a hair-follicle, (*s*) sebaceous gland.

5. [**Other Modes of Ending of Sensory Nerves.**—Some sensory nerves terminate not by means of special end-organs, but their axis-cylinder splits up into fibrils to form a nervous network, from which fine fibrils are given off to terminate in the tissue in which the nerve ends. These fibrils, as in the cornea (§ 384), terminate by means of free ends between the epithelium on the anterior surface of the cornea (fig. 753) and some observers state that the free ends are provided with small enlargements ("*boutons terminals*") (fig. 755, *a*). These enlargements or "**tactile cells**" occur in the nose of the guinea-pig and mole. A similar mode of termination occurs between the cells of the epidermis in man and mammals (fig. 357).]

[6. In **Hair-follicles.**—A medullated nerve-fibre passes to a hair-follicle immediately below the entrance of the duct of the sebaceous gland, where it loses its myelin and divides, giving rise to circular and longitudinal fibres. The longitudinal fibres, which are always inside the circular fibres, run towards the surface of the skin in the folds of the

vitreous lamina and end about the same level in flattened expansions, which, however, are best seen in a transverse section of a hair-follicle (*Ranvier*).]

7. Tendons, especially at their junction with muscles, have special end-organs (*Sachs, Rollett, Golgi*), which assume various forms ; it may be a network of primitive nerve-fibrils (fig. 383), or flattened end-flakes or plates in the sterno-radial muscle of the frog, or elongated oval end-bulbs, not unlike the end-bulbs of the conjunctiva, or small simple Pacinian corpuscles.

Prus found ganglion cells more frequently in the subcutaneous tissue than in the corium, and they appeared to have some relation to the blood-vessels and sweat-glands.

425. **SENSORY AND TACTILE SENSATIONS.**—In the sensory nerve-trunks there are two functionally different kinds of nerve-fibres :—(1) Those which administer to *painful* impressions, which are sensory nerves in the narrower sense of the word ; and (2) those which administer to tactile impressions and may therefore be called *tactile* nerves. The sensations of **temperature** and **pressure** are also reckoned as belonging to the tactile group. It is extremely probable that the sensory and tactile nerves have different end-organs and fibres, and that they have also special perceptive nerve-centres in the brain, although this is not definitely proved. This view, however, is supported by the following facts :—

1. That sensory and tactile impressions cannot be discharged at the same time from all the parts which are endowed with sensibility. Tactile sensations, including pressure and temperature, are only discharged from the coverings of the skin, the mouth, the entrance to the floor of the nose, the pharynx, the lower end of the rectum and genito-urinary orifices ; feeble indistinct sensations of temperature are felt in the œsophagus. Tactile sensations are absent from all internal viscera, as has been proved in man in cases of gastric, intestinal, and urinary fistulæ. Pain alone can be discharged from these organs. **2.** The conduction channels of the tactile and sensory nerves lie in different parts of the spinal cord (§ 364, 1 and 5). This renders probable the assumption that their central and peripheral ends also are different. **3.** Very probably the reflex acts discharged by both kinds of nerve-fibres—the tactile and pathic—are controlled, or even inhibited, by special central nerve-organs (§ 361). **4.** Under pathological conditions, and under the action of narcotics, the one sensation may be suppressed while the other is retained (§ 364, 5).

Sensory Stimuli.—In order to discharge a painful impression from sensory nerves, *relatively strong* stimuli are required. The stimuli may be mechanical, chemical, electrical, thermal, and somatic, the last being due to inflammation or anomalies of nutrition and the like.

Peripheral Reference of the Sensations.—These nerves are excitable along their entire course, and so is their central termination, so that pain may be produced by stimulating them in any part of their course, but this pain, according to the "**law of peripheral perception,**" is always referred to the periphery.

The tactile nerves can only discharge a tactile impression or sensation of contact when moderately strong mechanical pressure is exerted, while thermal stimuli are required to produce a temperature sensation, and in both cases, the results are obtained only when the appropriate stimuli are applied to the end-organs. If pressure or cold be applied to the *course* of a nerve-trunk, *e.g.*, to the ulna at the inner surface of the elbow-joint, we are conscious of painful sensations, but never of those of temperature, referable to the *peripheral* terminations of the nerves in the inner fingers. All strong stimuli disturb normal tactile sensations by over-stimulation, and hence cause pain.

The law of the specific energy of nerves leads us to assume that the cutaneous nerves contain different kinds of nerve-fibres with different kinds of end-organs, which subserve different kinds of impressions, *e.g.*, pressure, temperature, and pain. Blix and Goldscheider have found such differences. Electrical stimulation causes different sensations according to the part of the skin where it is applied ; at one

spot, pain only is produced, at another a sensation of cold, at a third a sensation of heat, and at a fourth a sensation of pressure. At every temperature point or spot, there is insensibility for pain or pressure. The "**pressure-points**" or pressure-spots lie much closer together, and are more numerous than the temperature-points. There are special "**pain-spots**" and even "tickling-spots." These spots are arranged in a linear chain, which usually radiates from the hair-follicles. The "tickling-spots" coincide with the pressure and pain-spots. The feeling of tickling corresponds to the feeblest stimulation of a nerve-fibre, and pain to the strongest. The pain-spots can be isolated by means of a needle, or electrically, especially in the cutaneous furrows, in which the pressure-sense is absent.

Goldscheider removed from his own body small pieces of skin, in which he had previously ascertained the presence of these "spots," and then investigated the exeised skin microscopically. At each such spot he found a rich supply of nerves ; at the pressure spots, there were no touch-corpuscles.

[By means of the skin, impressions are supplied also to the brain, whereby we become conscious of the amount and direction of a body moved in contact with the skin. Indeed, the discriminative sensibility is more acute for motion than for touch ; but the liability to error in judging of the distance and direction is great (*Hall*).]

[Very complex sensations are obtained by means of the combined action of the skin and muscles, *e.g.*, those known as "**feelings of double contact.**" These sensations are of the greatest advantage in acquiring the use of instruments and tools. If we touch an object with a rod, we seem to feel the object at the point of the rod, and not in the hand where the cutaneous nerves are actually stimulated. With a walking stick, we feel the ground at the end of the stick. Touch the tips of the hair, or a tooth, and the sensation is referred to the tips of the hair in the one case, and the crown of the tooth in the other (*Ladd*).]

426. SENSE OF LOCALITY.—We are not only able to distinguish differences of pressure or temperature by our sensory nerves, but we are able to distinguish the part which has been touched. This capacity is spoken of as the sense of space or **locality**.

Methods of Testing.—1. Place the two blunted points of a pair of compasses (fig. 757) upon the part of the skin to be investigated, and determine the smallest distance at which the two points are felt only as *one* impression. Sieveking's **æsthesiometer** may be used instead (fig. 758) ; one of the points is movable along a graduated rod, while the other is fixed. 2. The distance between the points of the instrument being kept the same, touch several parts of the skin, and ask if the person feels the impression of the points coming nearer to or going wider apart. 3. Touch a part of the skin with a blunt instrument, and observe if the spot touched is correctly indicated by the patient. 4. Separate the points of two pairs of compasses unequally, and place their points upon different parts of the skin, and ask the person to state when the points of both appear to be equally apart. A distance of 4 lines on the forehead appears to be equal to a distance of 2·4 lines on the upper lip. This is Fechner's "**method of equivalents.**"

Fig. 757.
Æsthesiometer.

The following results have been obtained. The sense of locality of a part of the skin is more acute under the following conditions:—

1. The greater the *number of tactile nerves* in the corresponding part of the skin.

2. The greater the *mobility of the part*, so that it increases in the extremities towards the fingers and toes. The sense of locality is always very acute in parts of the body that are very rapidly moved (*Vierordt*).

3. The sensibility of the limbs is finer in the *transverse axis* than in the long axis of the limb, to the extent of $\frac{1}{8}$th on the flexor surface of the upper limb, and $\frac{1}{4}$th on the extensor surface.

4. The *mode of application* of the points of the æsthesiometer:—(*a*) According as they are applied one after the other, instead of simultaneously, or as they are

considerably warmer or colder than the skin (*Klug*), a person may distinguish a less distance between the points. (*b*) If we begin with the points wide apart and approximate them, then we can distinguish a less distance than when we proceed from imperceptible distances to larger ones. (*c*) If the one point is warm and the other cold, on exceeding the next distance we feel two impressions, but we cannot rightly judge of their relative positions (*Czermak*).

5. *Exercise* greatly improves the sense of locality; hence the extraordinary acuteness of this sense in the blind, and the improvement always occurs on both sides of the body (*Volkmann*).

[Fr. Galton finds that the reputed increased acuteness of the other senses in the case of the blind is not so great as is generally alleged. He tested a large number of boys at an educational blind asylum, with the result that the performances of the blind boys were by no means superior to those of other boys. He points out, however, that "the guidance of the blind depends mainly on the multitude of collateral indications, to which they give much heed, and not in their superiority in any one of them."]

6. *Moistening* the skin with indifferent fluids increases the acuteness. If, however, the skin between two points, which are still felt as two distinct objects, be slightly tickled, or be traversed by an imperceptible electrical current, the impressions become fused (*Suslowa*). The sense of locality is rendered more acute at the

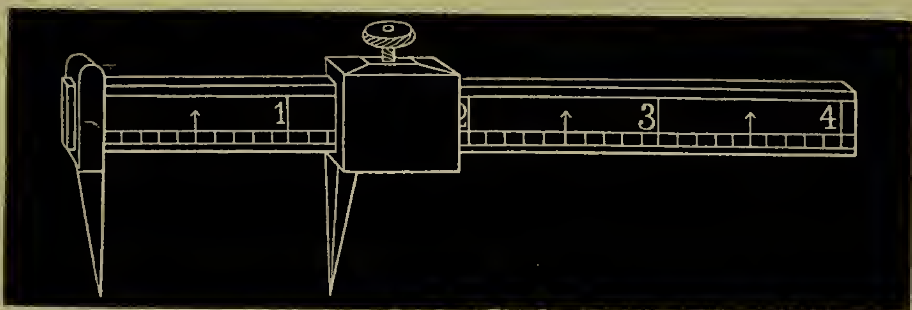


Fig. 758.

Æsthesiometer of Sieveking.

cathode when a constant current is used (*Suslowa*), and when the skin is congested by stimulation (*Klinkenberg*), and also by slight stretching of the skin (*Schmey*); further, by baths of carbonic acid (*v. Basch and v. Dietl*), or warm common salt, and temporarily by the use of caffein (*Rumpf*).

7. *Anæmia*, produced by elevating the limbs, or *venous hyperæmia* (by compressing the veins), blunts the sense, and so does too frequent testing of the sense of locality, by producing fatigue. The sense is also blunted by cold applied to the skin, the influence of the anode, strong stretching of the skin, as over the abdomen during pregnancy, previous exertion of the muscles under the part of the skin tested, and some poisons, *e.g.*, atropin, daturin, morphin, strychnin, alcohol, potassium bromide, cannabin, and chloral hydrate.

	Millimetres.		Millimetres.
Tip of tongue, ...	1·1 [1·1]	Ball of thumb, ...	6·5–7·
Third phalanx of finger, volar surface, ...	2·–2·3 [1·7]	Ball of little finger, . . .	5·5–6·
Red part of the lip, . . .	4·5 [3·9]	Centre of palm, . . .	8· –9·
Second phalanx of finger, volar surface, ...	4·–4·5 [3·9]	Dorsum and side of tongue, white of the lips, metacarpal part of the thumb, ...	9· [6·8]
First phalanx of finger, volar surface, ...	5·–5·5	Third phalanx of the great toe, plantar surface, . . .	11·3 [6·8]
Third phalanx of finger, dorsal surface, ...	6·8 [4·5]	Second phalanx of the fingers, dorsal surface, . . .	11·3 [9·]
Tip of nose, ...	6·8 [4·5]	Back, ...	11·3 [9·]
Head of metacarpal bone volar,	5·–6·8 [4·5]	Eyelid, ...	11·3 [9·]

	Millimetres.		Millimetres.
Centre of hard palate,	13·5 [11·3]	Vertex,	33·8 [22·6]
Lower third of the fore-arm, volar surface,	15·	Knee,	36·1 [31·6]
In front of the zygoma,	15·8 [11·3]	Sacrum, gluteal region,	44·6 [33·8]
Plantar surface of the great toe,	15·8 [9·]	Fore-arm and leg,	45·1 [33·8]
Inner surface of the lip,	20·3 [13·5]	Neck,	54·1 [36·1]
Behind the zygoma,	22·6 [15·8]	Back at the fifth dorsal vertebra, lower dorsal and lumbar region,	54·1
Forehead,	22·6 [18·]	Middle of the neck,	67·7
Occiput,	27·1 [22·6]	Upper arm, thigh, and centre of the back,	67·7 [31·6–40·6]
Back of the hand,	31·6 [22·6]		
Under the chin,	33·8 [22·6]		

Smallest Appreciable Distance.—The preceding statement gives the smallest distance, in *millimetres*, at which two points of a pair of compasses can still be distinguished as double by an adult. The corresponding numbers for a boy twelve years of age are given within brackets.

Illusions of the sense of locality occur very frequently; the most marked are:—(1) A uniform movement over a cutaneous surface appears to be quicker in those places which have the finest sense of locality. (2) If we merely *touch* the skin with the two points of an æsthesiometer, then they feel as if they were wider apart than when the two points are *moved along* the skin (*Fechner*). (3) A sphere, when touched with short rods, feels larger than when long rods are used (*Tourtual*). (4) When the fingers of one hand are crossed, a small pebble or sphere placed between them feels double (**Aristotle's experiment**). [When a pebble is rolled between the crossed index and middle finger (fig. 759, B), it feels as if two balls were present, but with the fingers uncrossed single.] (5) When pieces of skin are transplanted, *e.g.*, from the forehead, to form a nose, the person operated on feels, often for a long time, the new nasal part as if it were his forehead.

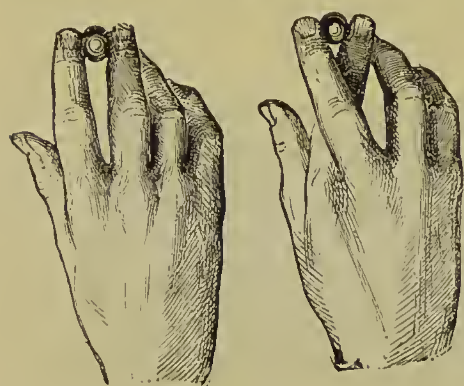


Fig. 759.
Aristotle's experiment.

Theoretical.—Numerous experiments were made by E. H. Weber, Lotze, Meissner, Czermak, and others to explain the phenomena of the sense of space. **Weber's theory** goes upon the assumption, that one and the same nerve-fibre proceeding from the brain to the skin can only take up one kind of impression, and administer thereto. He called the part of the skin to which each single nerve-fibre is distributed a "**circle of sensation.**" When two stimuli act simultaneously upon the tactile end-organ, then a double sensation is felt, when one or more circles of sensation lie between the two points stimulated. This explanation, based upon anatomical considerations, does not explain how it is that, with practice, the circles of sensation become smaller, and also how it is that only *one* sensation occurs, when both points of the instruments are so applied, that both points, although further apart than the diameter of a circle of sensation, at one time lie upon two adjoining circles, at another between two others with another circle intercalated between them.

Wundt's Theory.—In accordance with the conclusions of Lotze, Wundt proceeds from a psycho-physiological basis, that every part of the skin with tactile sensibility always conveys to the brain the *locality* of the sensation. Every cutaneous area, therefore, gives to the tactile sensation a "*local colour*" or quality, which is spoken of as the **local sign.** He assumes that this local colour diminishes from point to point of the skin. This gradation is very sudden in those parts of the skin where the sense of space is very acute, but occurs very gradually where the sense of space is more obtuse. Separate impressions unite into a common one, as soon as the gradation of the local colour becomes imperceptible. By practice and attention differences of sensation are experienced, which ordinarily are not observed, so that he explains the diminution of the circles of sensation by practice. The circle of sensation is an area of the skin, within which the local colour of the sensation changes so little that two separate impressions fuse into *one*.

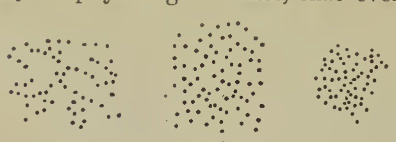


Fig 760.
Pressure-spots. *a* middle of the sole of the foot; *b*, skin of zygoma; *c*, skin of the back.

427. PRESSURE SENSE.—By the sense of pressure we obtain a knowledge of the amount of weight or pressure which is being exercised at the time on the different parts of the skin.

A specific end-apparatus arranged in a punctiform manner is connected with the pressure sense (fig. 760). These points or spots are called "**pressure-spots**" or "**pressure-points**" (*Blix*), and are endowed with varying degrees of sensibility; at some places (back, thigh) they are distinguished by a markedly pronounced after-sensation. The arrangement of the pressure-spots follows the type of the arrangement of the temperature-spots. The pressure-spots have usually another direction than that of hot and cold spots; as a rule, they are denser. The minimal distance at which two pressure-spots, when simultaneously stimulated, are felt as double, is —on the back, 4 to 6 mm.; breast, 0·8; abdomen, 1·5 to 2; cheek, 0·4 to 0·6; upper arm, 0·6 to 0·8; fore-arm, 0·5; back of the hand, 0·3 to 0·6; palm, 0·1 to 0·5; leg, 0·8 to 2; back of foot, 0·8 to 1; sole of foot, 0·8 to 1 mm.

Methods.—1. Place, on the part of the skin to be investigated, different **weights**, one after the other, and ascertain what perceptions they give rise to, and the sense of the difference of pressure to which they give rise. We must be careful to exclude differences of temperature and prevent the displacement of the weights—the weights must always be placed on the same spot, and the skin should be covered beforehand with a disc, while the muscular sense must be eliminated (§ 430). [This is done by supporting the hand or part of the skin which is being tested, so that the action of all the muscles is excluded.] 2. A process is attached to a balance and made to touch the skin, while by placing weights in the scale-pan or removing them, we test what differences in weight the person experimented on is able to distinguish (*Dohrn*). 3. In order to avoid the necessity of changing the weights, A. Eulenburg invented his **baræsthesiometer**, which is constructed on the same principle as a spiral spring paper-clip or balance. There is a small button which rests on the skin and is depressed by the spring. An index shows at once the pressure in grams, and the instrument is so arranged that the pressure can be very easily varied. 4. Goltz uses a **pulsating elastic tube**, in which he can produce waves of different height. He tested how high the latter must be before they are experienced as pulse-waves, when the tube is placed upon the skin. In estimating both the pressure sense and temperature sense, it is best to proceed on the principle of "**the least perceptible difference,**" *i.e.*, the different pressures or temperatures are graduated, either beginning with *great* differences, or proceeding from the *smallest* difference, and determining the limit at which the person can distinguish a difference in the sensation.

Results.—1. The *smallest perceptible pressure*, when applied to different parts of the skin, varies very greatly according to the locality. The greatest acuteness of sensibility is on the forehead, temples, and the back of the hand and fore-arm, which perceive a pressure of 0·002 grm.; the fingers first feel with a weight of 0·005 to 0·015 grm.; the chin, abdomen, and nose with 0·04 to 0·05 grm.; the finger nail 1 grm. (*Kammler and Aubert*).

The greater the sensibility of the skin, the more rapidly can stimuli succeed each other, and still be perceived as single impressions; 52 stimuli per second may be applied to the volar side of the upper arm, 61 on the back of the hand, 70 to the tips of the fingers, and still be felt singly (*Bloch*).

2. Intermittent variations of pressure, as in Goltz's tube, are felt more acutely by the tips of the fingers than with the forehead.

3. Differences between two weights are perceived by the tips of the fingers when the ratio is 29 : 30 (in the fore-arm as 18·2 : 20), provided the weights are not too light or too heavy. In passing from the use of very light to heavy weights, the acuteness or fineness of the perception of difference increases at once, but with heavier weights, the power of distinguishing differences rapidly diminishes again (*E. Hering, Biedermann*). This observation is at variance with the psycho-physical law of Fechner (§ 383).

4. A. Eulenburg found the following gradations in the fineness of the pressure sense:—The forehead, lips, dorsum of the cheeks, and temples appreciate differences of $\frac{1}{40}$ to $\frac{1}{30}$ (200 : 205 to 300 : 310 grm.). The dorsal surface of the last phalanx of the fingers, the fore-arm, hand, 1st and 2nd phalanx, the volar surface of the

hand, fore-arm, and upper arm, distinguish differences of $\frac{1}{10}$ to $\frac{1}{20}$ (200 : 220 to 220 : 210 grm.). The anterior surface of the leg and thigh are similar to the fore-arm. Then follow the dorsum of the foot and toes, the sole of the foot, and the posterior surface of the leg and thigh. Dohrn determined the smallest additional weight, which, when added to 1 grm. already resting on the skin, was appreciated as a difference, and he found that for the 3rd phalanx of the finger it was 0·499 grm.; back of the foot, 0·5 grm.; 2nd phalanx, 0·771 grm.; 1st phalanx, 0·02 grm.; leg, 1 grm.; back of the hand, 1·156 grm.; palm, 1·018 grm.; patella, 1·5 grm.; fore-arm, 1·99 grm.; umbilicus, 3·5 grms.; and the back, 3·8 grms. The small fine hairs of the skin are specially sensitive to pressure (*Blaschko*).

5. Too long time must not elapse between the application of two successive weights, but 100 seconds may elapse when the difference between the weights is 4 : 5 (*E. H. Weber*).

6. The sensation of an **after-pressure** is very marked, especially if the weight is considerable and has been applied for a length of time. But even light weights, when applied, must be separated by an interval of at least $\frac{1}{480}$ to $\frac{1}{610}$ second, in order to be perceived. When they are applied at shorter intervals, the sensations become fused. When Valentin pressed the tips of his fingers against a wheel provided with blunt teeth he felt the impression of a *smooth* margin, when the teeth were applied to the skin at the intervals above mentioned; when the wheel was rotated more slowly, each tooth gave rise to a distinct impression. Vibrations of strings are distinguished as such when the number of vibrations is 1506 to 1552 per second (*v. Wittich and Grünhagen*).

7. It is remarkable that pressure produced by the uniform compression of a part of the body, *e.g.*, by dipping a finger or arm in mercury, is not felt as such; the sensation is felt only at *the limit of the fluid*, on the volar surface of the finger, at the limit of the surface of the mercury.

428. TEMPERATURE SENSE.—The temperature sense makes us acquainted with the variations of the heat of the skin.

A specific end-apparatus arranged in a punctiform manner is connected with the temperature sense.

These "**temperature spots**" are arranged in a linear manner or in chains, which are usually slightly curved (figs. 761, 762, 763). They generally radiate from certain points of the skin, usually the hair-roots. The chain of the "**cold-spots**" usually does not coincide with those of the "**hot-spots,**" although the point from which they radiate may be the same. Frequently, these punctated lines are not complete, but they may be indicated by scattered points, between which, not unfrequently, points or spots for other qualities of sensation may be intercalated. Near the hairs there are almost always temperature-spots. In parts of the skin, where the temperature sensibility is slight, the temperature-points are present only near the hairs.

The sensation of cold occurs at once, while the sensation of heat develops gradually. Mechanical and electrical stimulation also excite the sensation of temperature. A gentle touch of the temperature-spots is not perceived; these points seem to be anæsthetic towards pressure and pain. As a general rule, the cold-spots are more abundant over the whole body—there are more of them in a given area—while the hot-spots may be quite absent. The hot-spots are, as a rule, perceived as double at a greater distance apart than the cold-spots. The minimal distance on the forehead is 0·8 mm. for the cold-spots and 4 to 5 mm. for the warm-spots; on the breast the corresponding numbers are 2 and 4 to 5; back, 1·5 to 2 and 4 to 6; back of hand, 2 to 3 and 3 to 4; palm, 0·8 to 2; thigh and leg, 2 to 3 and 3 to 4 mm.

To test the hot- and cold-spots, use a hot or cold metallic rod; at the cold-spots,

when they are lightly touched, only the sensation of cold will be felt, and a corresponding effect with a hot rod at the hot-spots. Both spots are insensible to objects of the same temperature as the skin.

According to E. Hering, what determines the sensation of temperature is the temperature of the thermic end-apparatus itself, *i.e.*, its zero-temperature. As often as the temperature of a cutaneous area is *above* its **zero-temperature**, we feel it as

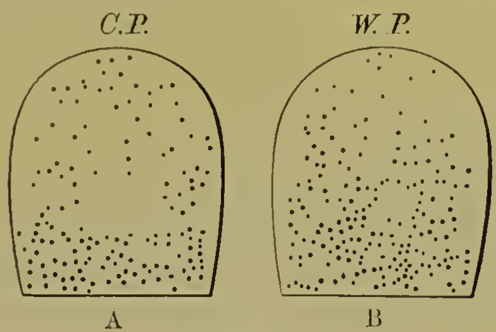


Fig. 761.

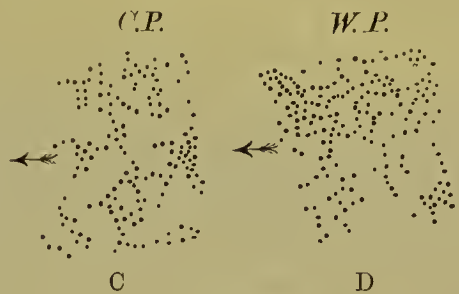


Fig. 762.

Fig. 761.—A, cold-spots, B, hot-spots, from the volar surface of the terminal phalanx of the index-finger to the margins of the nail. Fig. 762.—C, cold-spots, and D, warm-spots of the radial half of the dorsal surface of the wrist. The arrow indicates the direction in which the hair points.

warm; in the opposite case, *cold*. The one or the other sensation is more marked, the more the one or other temperature varies from the zero-temperature. The zero-temperature can undergo changes within considerable limits, owing to external conditions.

Methods of testing.—To the surface of the skin objects of the same size and with the same thermal conductivity are applied successively at different temperatures:—1. Nothnagel uses

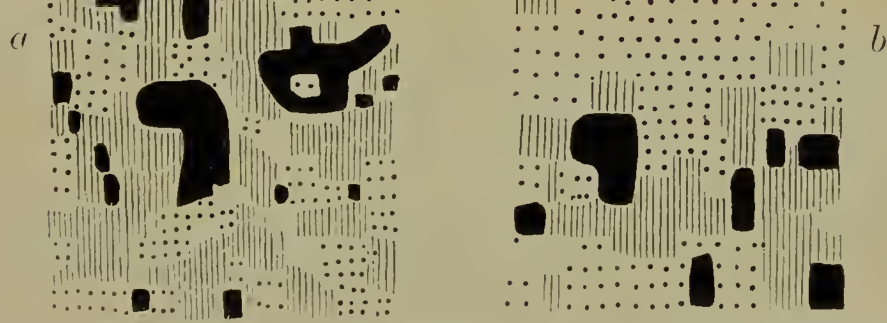


Fig. 763.

Cold- and hot-spots from the same part of the anterior surface of the fore-arm. *a*, cold-spots; *b*, hot-spots. The dark parts are the most sensitive, the hatched the medium, the dotted the feeble, and the vacant spaces the non-sensitive.

small wooden cups with a metallic base, and filled with warm and cold water, the temperature being registered by a thermometer placed in the cups. [2. Clinically, two test-tubes filled with cold and warm water, or two spoons, the one hot and the other cold, may be used.]

Results.—1. As a general rule, the feeling of cold is produced when a body applied to the skin robs it of heat; and, conversely, we have a sensation of warmth when heat is communicated to the skin.

2. The greater the thermal conductivity of the substance touching the skin, the more intense is the feeling of heat or cold (§ 218).

3. At a temperature of 15·5°–35° C., we distinguish distinctly differences of temperature of 0·2°–0·16° R. with the tips of the fingers (*E. H. Weber*). Temperatures just below that of the blood (33°–27° C.—*Nothnagel*) are distinguished most distinctly by the most sensitive parts, even to differences of 0·05° C. (*Lindermann*). Differences of temperature are less easily made out when dealing with temperatures of 33°–39° C., as well as between 14°–27° C. A temperature of 55° C., and also one a few degrees above zero (2·8° C.), cause distinct pain in addition to the sensation of temperature.

4. The sensibility for cold is generally greater than for warmth,—that of the left hand is greater than the right (*Goldscheider*). The different parts of the skin also vary in the acuteness of their thermal sense, and in the following order:—Tip of the tongue, eyelids, cheeks, lips, neck, and body. The perceptible minimum Nothnagel found to be 0·4° on the breast; 0·9° on the back; 0·3°, back of the hand; 0·4°, palm; 0·2°, arm; 0·4°, back of the foot; 0·5°, thigh; 0·6°, leg; 0·4°–0·2°, cheek; 0·4°–0·3° C., temple. The thermal sense is less acute in the middle line, *e.g.*, the nose, than on each side of it (*E. H. Weber*). Fig. 763 shows that in one and the same portion of skin, the cold- and hot-spots are differently located, *i.e.*, their different topography.

If the mucous membrane of the mouth be pencilled with a 10 per cent. solution of cocain, the sensibility for heat is abolished; the cooling sensation of menthol depends upon its stimulation of the cold nerves; CO_2 applied to the skin excites the heat-nerves (*Goldscheider*).

5. Differences of temperature are most easily perceived when the same part of the skin is affected successively by objects of different temperature. If, however, two different temperatures act simultaneously and side by side, the impressions are apt to become fused, especially when the two areas are very near each other.

6. Practice improves the temperature sense; congestion of venous blood in the skin diminishes it; diminution of the amount of blood in the skin improves it (*M. Alsberg*). When *large* areas of the skin are touched, the perception of differences is more acute than with small areas. Rapid variations of the temperature produce more intense sensations than gradual changes of temperature. Fatigue occurs soon.

Illusions are very common:—1. The sensations of heat and cold sometimes alternate in a paradoxical manner. When the skin is dipped first into water at 10° C. we feel cold, and if it be then dipped at once into water at 16° C., we have at first a feeling of warmth, but soon again of cold. 2. The same temperature applied to a large surface of the skin is estimated to be greater than when it is applied to a small area, *e.g.*, the whole hand when placed in water at 29°·5 C. feels warmer than when a finger is dipped into water at 32° C. 3. Cold weights are judged to be heavier than warm ones.

Pathological.—Tactile sensibility is only seldom *increased* (**hyperpselaphesia**), but great sensibility to differences of temperature is manifested by areas of the skin whose epidermis is partly removed or altered by vesicants or herpes zoster, and the same occurs in some cases of locomotor ataxia; while the sense of locality is rendered more acute in the two former cases and in erysipelas. An abnormal condition of the sense of locality was described by Brown-Séquard, where three points were felt when only two were applied, and two when one was applied to the skin. Landois finds that in himself pricking the skin of the sternum over the angle of Ludovicus is always accompanied by a sensation in the knee. [Some persons, when cold water is applied to the scalp, have a sensation referable to the skin of the loins (*Stirling*).] A remarkable variation of the sense of locality occurs in moderate poisoning with morphia, where the person feels himself abnormally large or greatly diminished. In degeneration of the posterior columns of the cord, Obersteiner observed that the patient was unable to say whether his right or left side was touched ("**allochiria**"). Ferrier observed a case where a stimulus applied to the right side was referred to the left, and *vice versâ*.

Diminution and paralysis of the tactile sense (**Hypopselaphesia** and **Apselaphesia**) occur either in conjunction with simultaneous injury to the sensory nerves, or alone. It is rare to find that one of the qualities of the tactile sense is lost, *e.g.*, either the tactile sense or the sense of temperature—a condition which has been called "*partial tactile paralysis.*" Limbs which are "*sleeping*" feel heat and not cold (*Herzen*).

429. **COMMON SENSATION—PAIN.**—By the term **common sensation** we understand pleasant or unpleasant sensations in those parts of our bodies which are endowed with sensibility, and which are not referable to external objects, and whose characters are difficult to describe, and cannot be compared with other sensations. Each sensation is, as it were, a peculiar one. To this belong pain, hunger, thirst, malaise, fatigue, horror, vertigo, tickling, well-being, illness, the respiratory feeling of free or impeded breathing.

Pain may occur wherever sensory nerves are distributed, and it is invariably caused by a stronger stimulus than normal being applied to sensory nerves. Every kind of stimulation, mechanical, thermal, chemical, electrical as well as somatic (inflammation or disturbances of nutrition), may excite pain. The last appears to be especially active, as many tissues become extremely painful during inflammation (*e.g.*, muscles and bones), while they are comparatively insensible to cutting. Pain may be produced by stimulating a sensory nerve in any part of its course, from its centre to the periphery, but the sensation is invariably referred to the peripheral end of the nerve. This is the **law of the peripheral reference of sensations.** Hence, stimulation of a nerve, as in the scar of an amputated limb, may give rise to a sensation of pain which is referred to the parts already removed. Too violent stimulation of a sensory nerve in its course may render it incapable of conducting impressions, so that peripheral impressions are no longer perceived. If a sufficient stimulus to produce pain be then applied to the central part of the nerve, such an impression is still referred to the peripheral end of the nerve. Thus we explain the paradoxical **anæsthesia dolorosa.** In connection with painful impressions, the patient is often unable to localise them exactly. This is most easily done when a small injury (prick of a needle) is made on a peripheral part. When, however, the stimulation occurs in the course of the nerve, or in the centre, or in nerves whose peripheral ends are not accessible, as in the intestines, pain (as belly-ache), which cannot easily be localised, is the result.

Irradiation of pain.—During violent pain there is not unfrequently irradiation of the pain (§ 364, 5), whereby localisation is impossible. It is rare for pain to remain continuous and uniform; more generally there are exacerbations and diminutions of the intensity, and sometimes *periodic* intensification, as in some neuralgias.

The **intensity of the pain** depends especially upon the excitability of the sensory nerves. There are considerable individual variations in this respect, some nerves, *e.g.*, the trigeminus and splanchnic, being very sensitive. The larger the number of fibres affected the more severe the pain. The duration is also of importance, in as far as the same stimulation, when long continued, may become unbearable. We speak of piercing, cutting, boring, burning, throbbing, pressing, gnawing, dull, and other kinds of pain, but we are quite unacquainted with the conditions on which such different sensations depend. Painful impressions are abolished by **anæsthetics** and **narcotics**, such as ether, chloroform, morphia, &c. (§ 364, 5).

Methods of Testing.—To test the cutaneous sensibility, we usually employ the constant or induced electrical current. Determine first the *minimum sensibility*, *i.e.*, the strength of the current which excites the first trace of sensation, and also the *minimum of pain*, *i.e.*, the feeblest strength of the current which first causes distinct impressions of pain. The electrodes consist of thin metallic needles, and are placed 1 to 2 cm. apart.

Pathological.—When the excitability of the nerves which administer to painful sensations is increased, a slight touch of the skin, nay, even a breath of cold air, may excite the most violent

pain, constituting **cutaneous hyperalgia**, especially in inflammatory or exanthematic conditions of the skin. The term **cutaneous paralgia** is applied to certain anomalous, disagreeable, or painful sensations which are frequently referred to the skin—itching, creeping, formication, cold, and burning. In cerebro-spinal meningitis, sometimes a prick in the sole of the foot produces a double sensation of pain and a double reflex contraction. Perhaps this condition may be explained by supposing that in a part of the nerve the condition is delayed (§ 337, 2). In **neuralgia** there is severe pain, occurring in paroxysms, with violent exacerbations and pain shooting into other parts (p. 733). Very frequently excessive pain is produced by pressure on the nerve where it makes its exit from a foramen or traverses a fascia.

Valleix's Points Douloureux (1841).—The skin itself to which the sensory nerve runs, especially at first, may be very sensitive; and when the neuralgia is of long duration the sensibility may be diminished even to the condition of analgesia (*Türck*); in the latter case there may be pronounced anæsthesia dolorosa (p. 1025).

Diminution or **paralysis** of the sense of pain (**hypalgia** and **analgia**) may be due to affections of the ends of the nerves, or of their course, or central terminations.

Metalloscopy.—In hysterical patients suffering from hemianæsthesia, it is found that the feeling of the paralysed side is restored, when small metallic plates or larger pieces of different metals are applied to the affected parts (*Burcq, Charcot*). At the same time that the affected part recovers its sensibility the opposite limb or side becomes anæsthetic. This condition has been spoken of as transference of sensibility. The phenomenon is not due to galvanic currents developed by the metals; but it may be, perhaps, explained by the fact that, under physiological conditions, and in a healthy person, every increase of the sensibility on one side of the body, produced by the application of warm metallic plates or bandages, is followed by a diminution of the sensibility of the opposite side. Conversely, it is found that when one side of the body is rendered less sensitive by the application of cold plates, the homologous part of the other side becomes more sensitive (*Rumpf*).

430. MUSCULAR SENSE.—Muscular Sensibility.—The sensory nerves of the muscles (§ 292) always convey to us impressions as to the activity or non-activity of these organs, and in the former case, these impressions enable us to judge of the degree of contraction. It also informs us of the amount of the contraction to be employed to overcome resistance. Obviously, the muscular sense must be largely supported and aided by the sense of pressure, and conversely. E. H. Weber showed, however, that the muscle sense is finer than the pressure sense, as by it we can distinguish weights in the ratio of 39 : 40, while the pressure sense only enables us to distinguish those in the ratio of 29 : 30. In some cases there has been observed total cutaneous insensibility, while the muscular sense was retained completely. A frog deprived of its skin can spring without any apparent disturbance. The muscular sense is also greatly aided by the sensibility of the joints, bones, and fasciæ. Many muscles, *e.g.*, those of respiration, have only slight muscular sensibility, while it seems to be absent normally in the heart and non-striped muscle.

[The muscular sense stands midway between special and common sensations, and by it we obtain a knowledge of the condition of our muscles, and to what extent they are contracted; also the position of the various parts of our bodies and the resistance offered by external objects. Thus, sensations accompanying muscular movement are two-fold—(*a*) the movements in the unopposed muscles, as the movements of the limbs in space; and (*b*) those of resistance where there is opposition to the movement, as in lifting a weight. In the latter case the sensations due to innervation are important, and of course in such cases we have also to take into account the sensations obtained from mere pressure upon the skin. Our sensations derived from muscular movements depend on the *direction and duration* of the movements. On the sensations thus conveyed to the sensorium, we form judgments as to the direction of a point in space, as well as of the distance between two points in space. This is very marked in the case of the ocular muscles. It is also evident that the muscular sense is intimately related to, and often combined with, the exercise of the sensation of touch and sight (*Sully*).]

Methods of Testing.—Weights are wrapped in a towel and suspended to the part to be tested. The patient estimates the weight by raising and lowering it. The *electro-muscular*

sensibility also may be proved thus: cause the muscles to contract by means of induction shocks, and observe the sensation thereby produced. [Direct the patient to place his feet together while standing, and then close his eyes. A healthy person can stand quite steady, but in one with the muscular sense impaired, as in locomotor ataxia, the patient may move to and fro, or even fall (§ 346, 3). Again, a person with his muscular sense impaired may not be able to touch accurately and at once some part of his body, when his eyes are closed.]

A healthy person perceives a weight of 1 gram applied to his upper arm; when a weight of 15 grms. is applied, he perceives an addition of 1 gram. If the original weight be 50 grms., he will detect the addition of 2 grms.; if the original weight be 100 grms., he will detect 3 grms. The weight detectable by the individual finger varies. With the leg, when the weight is applied at the knee, the individual may detect 30 to 40 grms.; but sometimes only a greater weight. Often one can detect a difference of 10 to 20, or 30 to 70 grms.

Section of a sensory nerve causes disturbance of the fine graduation of movement (p. 755). Meynert supposes that the cerebral **centre** for muscular sensibility lies in the motor cortical centres, the muscles being connected by motor and sensory paths with the ganglionic cells in these centres.

Too severe muscular exercise causes the sensation of **fatigue**, *oppression*, and *weight* in the limbs (§ 304).

Illusions of the muscular sense.—A weight held by one limb appears to us to become lighter as soon as we contract other muscles of the limb, which, however, are not required to act in supporting the weight (*Charpentier*). If the tip of the tongue be pressed against a gap in the dental arch and then be moved to and fro, one has a feeling as if the teeth move with the movements of the tongue.

Pathological.—Abnormal increase of the muscular sense is rare (*muscular hyperalgia and hyperæsthesia*), as in *anxietas tibiarum*, a painful condition of unrest which leads to a continual change in the position of the limbs. In **cramp** there is intense pain, due to stimulation of the sensory nerves of the muscle, and the same is the case in inflammation. *Diminution* of the muscular sensibility occurs in some choreic and ataxic persons (§ 364, 5). In locomotor ataxia the muscular sense of the upper extremities may be normal or weakened, while it is usually considerably diminished in the legs. [The muscular sense is said to be increased in the hypnotic condition, and in somnambulists.]

Reproduction and Development.

431. **FORMS OF REPRODUCTION.—I. Abiogenesis** (Generatio aequivoca, sive spontanea, **spontaneous generation**).—It was formerly assumed that, under certain circumstances, non-living matter derived from the decomposition of organic materials became changed spontaneously into living beings. While Aristotle ascribed this mode of origin to insects, the recent observers who advocate this form of generation restrict its action solely to the lowest organisms. Experimental evidence is distinctly against spontaneous generation. If organised matter be heated to a very high temperature in sealed tubes, and be thus deprived of all living organisms or their spores, there is no generation of any organism. Hence, the dictum "Omne vivum ex ovo" (*Harvey*, or, ex vivo). Some highly organised invertebrate animals (Gordius, Anguillula, Tardigrada, and Rotatoria) may be dried, and even heated to 140° C., and yet regain their vital activities on being moistened (**Anabiosis**).

II. Division or **fission** occurs in many protozoa (amœba, infusoria). The organism, just as is the case with cells, divides, the nucleus when present taking an active part in the process, so that two nuclei and two masses of protoplasm forming two organisms are produced. The Ophidiasters amongst the echinoderms divide spontaneously, and they are said to throw off an arm which may develop into a complete animal. According to Trembley (1744), the hydra may be divided into pieces, and each piece gives rise to a new individual [although under normal circumstances the hydra gives off buds, and is provided with generative organs].

III. Budding or **gemmation** occurs in a well-marked form among the polyps and in some infusorians (Vorticella). A bud is given off by the parent, and gradually comes more and more to resemble the latter. The bud either remains permanently attached to the parent, so that a complex organism is produced, in which the digestive organs communicate with each other directly, or in some cases there may be a "colony" with a common nervous system, such as the polyzoa. In some composite animals (siphonophora) the different polyps perform different functions. Some have a digestive, others a motor, and a third a generative function, so that there is a physiological division of labour. Buds which are given off from the parent are formed internally in the rhizopoda. In some animals (polyps, infusoria), which can reproduce themselves by buds or division, there is also the formation of male and female elements of generation, so that they have a sexual and a non-sexual mode of reproduction.

IV. Conjugation is a form of reproduction which leads up to the sexual form. It occurs in the unicellular Gregarinæ. The anterior end of one such organism unites with the posterior end of another; both become encysted, and form *one* passive spherical body. The conjoined structures form an amorphous mass, from which numerous globular bodies are formed, and in each of which numerous oblong structures—the pseudo-navicelli—are developed. These bodies become, or give rise to an amœboid structure, which forms a nucleus and an envelope and becomes transformed into a gregarina.

Sexual reproduction requires the formation of the embryo from the conjunction of the male and female reproductive elements, the **sperm-cell** and the **germ-cell**. These products may be formed either in *one* individual (hermaphroditism, as in the flat worms and gasteropods), or in *two* separate organisms (male or female). Sexual reproduction embraces the following varieties:—

V. Metamorphosis is that form of sexual reproduction in which the embryo from an early period undergoes a series of marked changes of external form, *e.g.*, the chrysalis stage, and the

pupa stage, and in none of these stages is reproduction possible. Lastly, the final sexually developed form (the imago stage in butterflies) is produced, which forms the sexual products whose union gives rise to organisms which repeat the same cycle of changes. Metamorphosis occurs extensively amongst the insects ; some of them have several stages (holo-metabolic), and others have few stages (hemi-metabolic). It also occurs in some arthropoda, and worms, *e.g.*, trichina ; the sexual form of the animal occurs in the intestine, the numerous *larvæ* wander into the muscles, where they become encysted, and form undeveloped sexual organs, constituting the pupa stage of the muscular trichina. When the encysted form is eaten by another animal, the sexual organs come into activity, a new brood is formed, and the cycle is repeated. Metamorphosis also occurs in the frog and in petromyzon. [This is really a condition in which the embryo undergoes marked changes of form before it becomes sexually mature.]

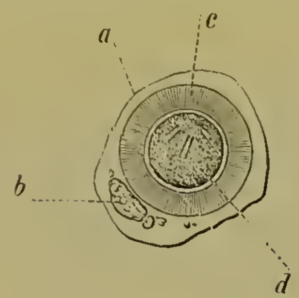


Fig. 764.

A ripe egg taken from the uterus of Tænia solium. *a*, Albuminous envelope ; *b*, remains of the yelk ; *c*, covering of the embryo; *d*, embryo with embryonal hooklets.

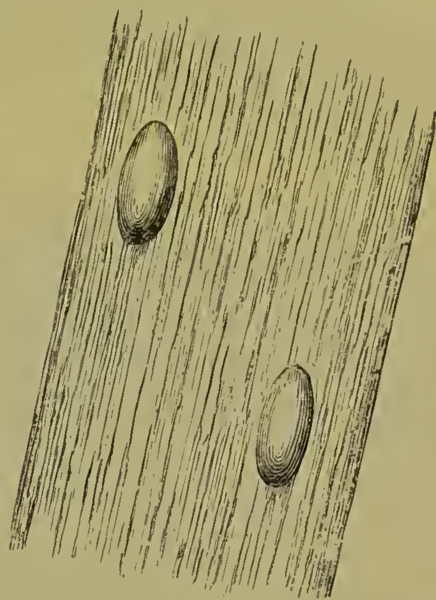


Fig. 765.

Encapsuled cysticercus from Tænia solium embedded in a human sartorius. Natural size.

VI. Alteration of Generations or Metagenesis.—(*Steenstrup*). — In this variety some of the members of the cycle can produce new beings non-sexually, while in the final stage reproduction is always sexual. From a medical point of view, the life-history of the **tape-worm** or **Tænia** is most important. The segments of the tape-worm are called **proglottides** (fig. 770), and each segment is hermaphrodite with testes, vas deferens, penis, ovary, &c., and numerous ova. The segments are evacuated with the fæces. The eggs are fertilised after they are shed (fig. 764), and from them is developed an elliptical **embryo**, provided with six hooklets, which is swallowed

Fig. 766.

Head of Tænia solium (I) and medio-canellata (II), and joints of both (1, 2).

by another animal, the host. These embryos bore their way into the tissues of the host, where they undergo development, forming the encysted stage, Cysticercus (fig. 767), Coenurus, or Echinococcus (fig. 768). The encysted capsule may contain one (cysticercus) or many (coenurus)

sessile heads of the tænia. In order to undergo further development, the cysticercus must be eaten alive by another animal, when the head or **scolex** fixes itself by the hooklets and suckers to the intestine of its new host (fig. 767), where it begins to bud and produce a series of new segments between the head and the last-formed segment, and thus the cycle is repeated.

The most important flat-worms are :—**Tænia solium**, in man ; the Cysticercus cellulosæ (fig. 766), in the pig, when it constitutes the *measle* in pork ; **Tænia mediocanellata** (fig. 770), the encysted stage, in the ox ; **Tænia coenurus**, in the dog's intestine ; the encysted stage, or Coenurus cerebralis, in the brain of the sheep, where it gives rise to the condition of "staggers" ; **Tænia echinococcus**, in the dog's intestine ; the embryos or scolices occur in the liver of man as "**hydatids.**"

The medusæ also exhibit alternation of generations, and so do some insects, especially the plant lice or aphides.

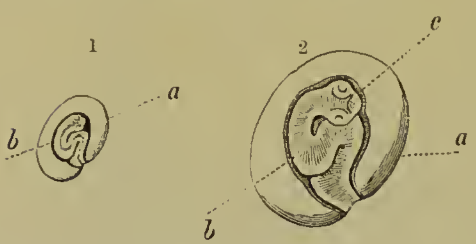


Fig. 767.

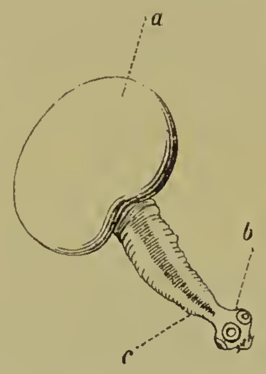


Fig. 768.

Fig. 769.

Fig. 767.—Cysticerci from Tænia solium removed from their capsule. 1, natural size ; 2, magnified. *a*, embryo-sac ; *b*, cavity produced by budding of the embryo-sac ; *c*, suctorial discs and hooklets. Fig. 768.—Cysticercus of Tænia solium, with its head and segments protruded. *a*, caudal-sac ; *b*, head of the tape-worm, with discs and hooklets (scolex) ; *c*, neck. Fig. 769.—Part of an Echinococcus capsule, with developing buds. *a*, sheath ; *b*, parenchymatous layer ; *c*, germinating capsule filled with scolices.

VII. Parthenogenesis (*Owen, v. Siebold*).—In this variety, in addition to sexual reproduction, new individuals may be produced without sexual union. The non-sexually produced brood is always of one sex, as in the bees. A beehive contains a queen, the workers, and the drones or males. During the nuptial flight the queen is impregnated by the males, and the seminal fluid is stored up in the receptaculum seminis of the queen, and it appears that the queen may voluntarily permit the contact of this fluid with the ova or withhold it. All fertilised eggs give rise to female, and all unfertilised ones to male bees.

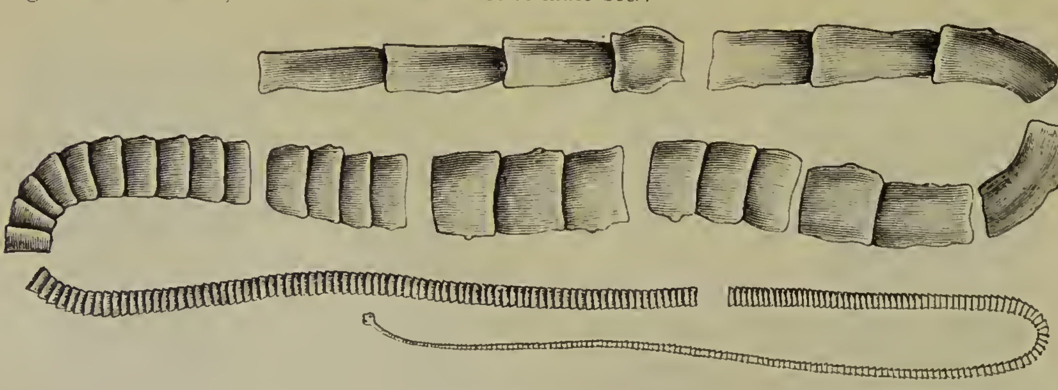


Fig. 770.

Fig 770.—Tænia mediocanellata. Natural size.

VIII. Sexual reproduction without any intermediate stages occurs in, besides man, mammals, birds, reptiles, and most fishes.

432. TESTIS—SEMINAL FLUID.—In the **testis**, or male reproductive organ, the seminal fluid which contains the male element or spermatozoa is formed. The **framework** of the gland consists of a thick strong white fibrous covering, the **tunica albuginea**, composed chiefly of white interlacing fibrous tissue. Externally,

this layer is covered by the visceral layer of the serous membrane, or the **tunica vaginalis**, which invests the testis and epididymis. The tunica albuginea is prolonged for some distance as a vertical septum into the posterior part of the testis, to form the **mediastinum testis** or **corpus Highmori**. **Septa** or trabeculæ—more or less complete—stretch from the under surface of the T. albuginea towards the mediastinum, so that the organ is subdivided thereby into a number of **compartments** or **lobules**, with their bases directed outwards and their apices towards the mediastinum. From these, finer sustentacular fibres pass into the compartments to support the structures lying in these compartments.]

[**Arrangement of Tubules.**—Each compartment contains several **seminal tubules**, long convoluted tubules ($\frac{1}{100}$ in. in diam.) which rarely branch except at their outer end; they are about 2 feet in length and exceed 800 in number. These tubules run towards the mediastinum, those in one compartment uniting at an acute angle with each other, to form a smaller number of narrower straight tubules—**tubuli recti** (fig. 771). These straight tubules open into a network of tubules in the mediastinum to form the **rete testis**, a dense network of tubules of irregular diameter (fig. 771). From this network there proceed 12 to 15 wider ducts,—the **vasa efferentia**—which after emerging from the testis are at first straight, but soon become convoluted—and form a series of conical eminences — the **coni vasculosi**—which together form the head of the **epididymis**. These tubes gradually unite with each other and form the body and globus minor of the **epididymis**, which, when unravelled, is a tube about 20 feet long terminating in the **vas deferens** (2 feet long), which is the excretory duct of the testis.]

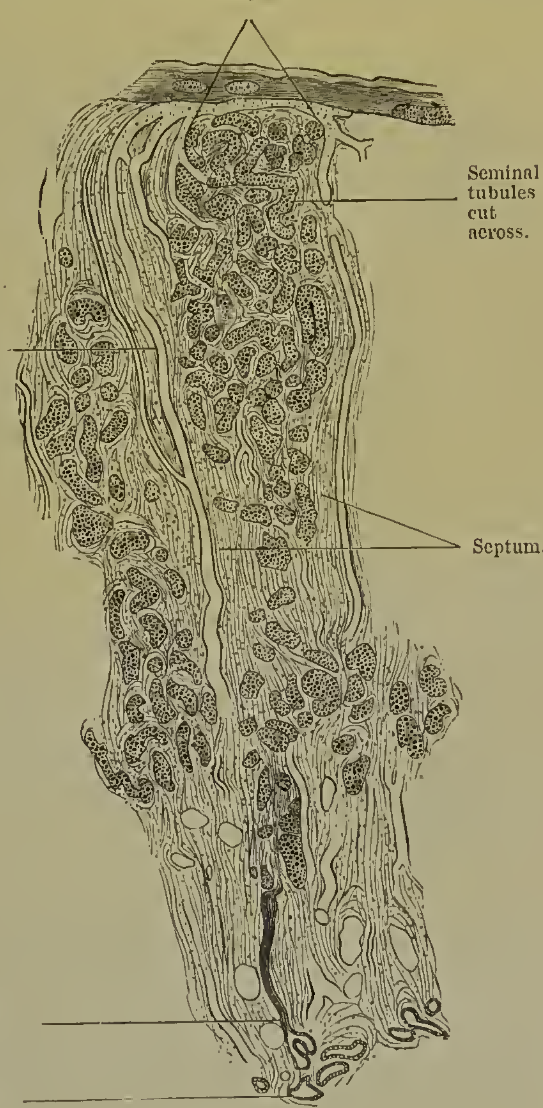


Fig. 771.
Transverse section of the testis (low power view).

[**Structure of a Seminal Tubule.**—The **seminal tubules** consist of a thick well-marked basement membrane, composed of flattened nucleated cells arranged like membranes (fig. 776). These tubes are lined by several layers of more or less cubical cells; there is an **outer** row of such cells next the basement membrane, and often showing a dividing large nucleus. Internal to these are several layers of **inner** large clear cells, with nuclei often dividing, so that they form many

daughter cells which lie internal to them and next the lumen. From these daughter cells are formed the spermatozoa, and they constitute the **spermatoblasts**. These several layers of cells leave a distinct lumen. The **tubuli recti** are narrow in diameter, and lined by a single layer of squamous or flattened epithelium (fig. 772). The **rete testis** consists merely of channels in the fibrous stroma without a distinct membrana propria, but lined by flattened epithelium. The **vasa efferentia** and **coni vasculosi** have circular smooth muscular fibres in their walls, and are lined by a layer of columnar ciliated epithelium with striated protoplasm. At the bases of these cells in some parts is a layer of smaller granular cells. These tubules form the **epididymis**, whose tubules have the same structure (fig. 773). In the sheep, pigment cells are often found in the basement membrane.]

[The **vas deferens** is lined by several layers of columnar epithelium resting on a dense layer of fibrous tissue—the **mucosa**. Outside this is the **muscular coat**, a thick layer of non-striped muscle, composed of a thick inner *circular*, and thick outer *longitudinal* layer, a thin sub-mucous coat connecting the muscular and mucous coats together; outside all is the fibrous **adventitia**.]

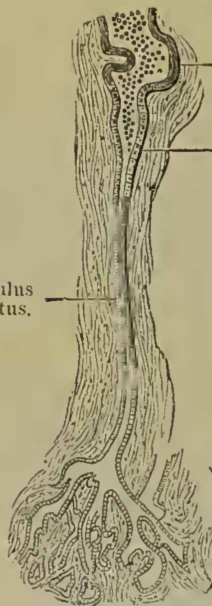


Fig. 772.

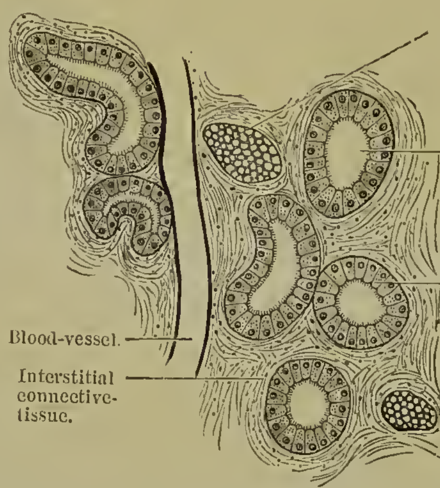


Fig. 773.

Fig. 772.—Convoluted seminal tubule opening into a narrow straight tubule. Fig. 773.—Transverse section of the tubules of the epididymis.

[The **interstitial tissue** (fig. 771), supporting the seminal tubules, is laminated and covered by endothelial plates, with slits or spaces between the lamellæ, which form the origin of the **lymphatics**. These lymph-spaces are easily injected by the puncture method. In fact, if Berlin blue be forced into the testis, the lymphatics of the testis and spermatic cord are readily filled with the injection. In some animals (boar), and to a less extent in man, dog, there are also fairly large polyhedral **interstitial cells**, often with a large nucleus and sometimes pigmented. They represent the residue of the epithelial cells of the Wolffian bodies (*Klein*), or, according to Waldeyer, they are plasma cells. The **blood-vessels** are numerous, and form a dense plexus outside the basement membrane of the seminal tubules.]

Chemical Composition.—The **seminal fluid**, as discharged from the urethra, is mixed with the secretion of the glands of the vas deferens, Cowper's glands, and those of the prostate, and with the fluid of the vesiculæ seminales. Its **reaction** is neutral or alkaline, and it contains 82 per cent. of water, serum-albumin alkali-

albuminate, nuclein, lecithin, cholesterin, fats (protamin ?), phosphorised fat, salts (2 per cent.), especially phosphates of the alkalies and earths, together with sulphates, carbonates, and chlorides. The odorous body, whose nature is unknown, was called "**spermatin**" by Vauquelin.

Seminal fluid.—The sticky, whitish-yellow seminal fluid, largely composed of a mixture of the secretions of the above-named glands, when exposed to the air, becomes more fluid, and on adding water it becomes gelatinous, and from it separate whitish transparent flakes. When long exposed, it forms rhomboidal crystals, which, according to Schreiner, consist of phosphatic salts with an organic base (C_2H_5N). These **crystals** (fig. 774) are said to be derived from the prostatic fluid, and are identical with the so-called Charcot's crystals (fig. 171, *c*, and § 138). The **prostatic fluid** is thin, milky, amphoteric, or of slightly acid reaction, and is possessed of the seminal odour. The phosphoric acid necessary for the formation of the crystals is obtained from the seminal fluid. A somewhat similar odour occurs in the albumin of eggs not quite fresh. The non-poisonous ptomain, cadaverin (pentamethyldiamin of *Ladenburg*), isolated by Brieger from dead bodies, has a similar odour. The secretion of the vesiculæ seminales of the guinea-pig contains much fibrinogen (p. 465).

Fig. 774.
Crystals from spermatic fluid.

The **spermatozoa** are 50 μ long, and consist of a flattened pear-shaped **head** (fig. 775, 1 and 2, *k*), which is followed by a rod-shaped **middle piece**, *m* (*Schweigger-Seidel*), and a long tail-like prolongation or **cilium**, *f*. The spermatozoon is propelled forwards by the to-and-fro movements of the tail at the rate of 0·05 to 0·5 mm. per second; the movement is most rapid immediately after the fluid is shed, but it gradually becomes feebler.

Finer Structure of Spermatozoa.—The observations of Jensen have shown that the middle piece and head are still more complex, although this is not the case in human spermatozoa and those of the bull (*G. Retzius*). These consist of a flattened, long, narrow, transparent, protoplasmic mass, with a fibre composed of many delicate threads in both margins. At the tip of the tail both fibres unite into one. The fibre of the one margin is generally straight, the other is thrown into wave-like folds, or winds in a spiral manner round the other (*W. Krause, Gibbes*). G. Retzius describes a special terminal filament (fig. 775, *e*). An axial thread surrounded by an envelope of protoplasm, traverses the middle piece and the tail (*Eimer, v. Braun*). [Leydig showed that in the salamander there is a delicate membrane attached to the tail, and Gibbes has described a spiral thread attached to the head (newt) and connected with the middle piece by a hyaline membrane.]

Motion of the Spermatozoa.—[After the discharge of the seminal fluid, the spermatozoa exhibit spontaneous movements for many hours or days.] The movements are due to the lashing movements of the tail, which moves in a circle or rotates on its long axis, the impulse to movement proceeding from the protoplasm of the middle piece and the tail, which seem to be capable of moving when they are detached (*Eimer*). These movements are comparable to those that occur in cilia (§ 292), and there are transition forms between ciliary and amœboid movements, as in the Monera. **Action of Reagents on Spermatozoa.**—Within the testis they do not exhibit movement, as the fluid is not sufficiently dilute to permit them to move. Their movements are specially lively in the normal secretion of the female sexual organs (*Bischoff*), and they move pretty freely, and for a long time, in all normal animal secretions except saliva. Their movements are paralysed by water, alcohol, ether, chloroform, creosote, gum, dextrin, vegetable mucin, syrup of grape-sugar, or very alkaline or acid uterine or vaginal mucus (*Donné*), acids and metallic salts, and a too high or too low temperature. The narcotics, as long as they are chemically indifferent, behave as indifferent fluids, and so do medium solutions of urea, sugar, albumin, common salt, glycerin, amygdalin, &c.; but if these be too dilute or too concentrated, they alter the amount of water in the spermatozoa and paralyse them. The quiescence produced by water may be set aside by dilute alkalies (*Virchow*), as with cilia (p. 560). En-

gelmann finds that minute traces of acids, alcohol, and ether excite movements. The spermatozoa of the frog may be frozen four times in succession without killing them. They bear a heat of 43°·75 C., and they will live for 70 days when placed in the abdominal cavity of another frog (*Mantegazza*).

Resistance.—Owing to the large amounts of earthy salts which they contain, when dried upon a microscopical slide, they still retain their form (*Valentin*). Their form is not destroyed by nitric, sulphuric, hydrochloric, or boiling acetic acid, or by caustic alkalies; solutions of NaCl and saltpetre (10 to 15 per cent.) change them into amorphous masses. Their organic basis resembles the semi-solid albumin of epithelium.

Seminal fluid, besides spermatozoa, also contains **seminal cells**, a few epithelial cells from the seminal passages, numerous lecithin granules, stratified amyloid bodies (inconstant), granular yellow pigment, especially in old age, leucocytes, and **sperma crystals** (*Fürbinger*).

Development of Spermatozoa.—The walls of the seminal tubules, *n*, which are made up of spindle-shaped cells, are lined by a nucleated, protoplasmic layer (fig.

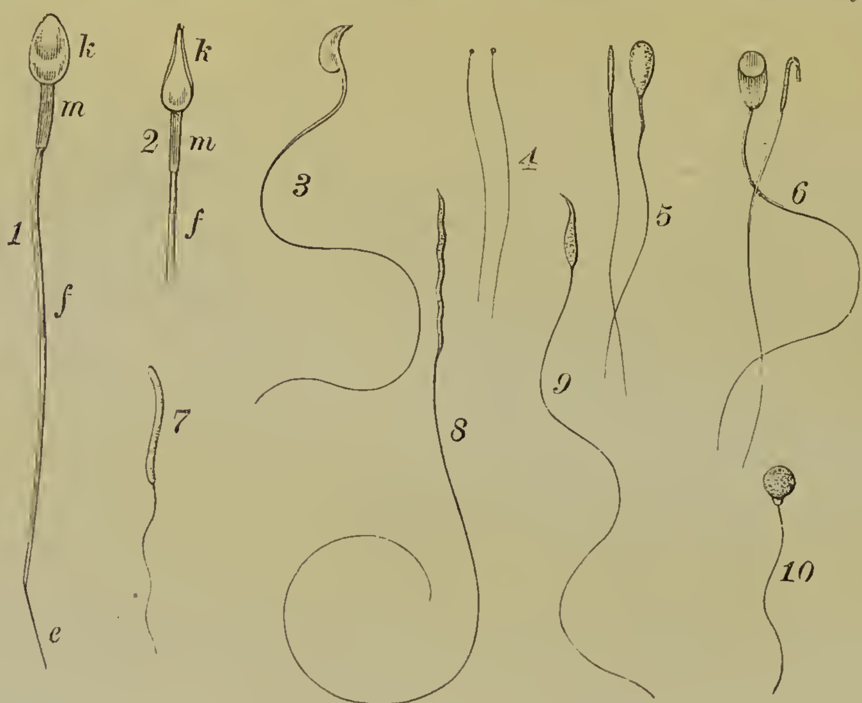


Fig. 775.

Spermatozoa. 1, human (× 600), the head seen from the side ; 2, on edge ; *k*, head ; *m*, middle piece ; *f*, tail ; *e*, terminal filament ; 3, from the mouse ; 4, bothriocephalus latus ; 5, deer ; 6, mole ; 7, green woodpecker ; 8, black swan ; 9, from a cross between a goldfinch (M) and a canary (F) ; 10, from cobitis.

776, I, *b*, and IV, *h*), from which, according to one view, there project into the lumen of the tube long (0·053 mm.) column-like prolongations (I, *c*, and II, III, IV), which break up at their free end into several round or oval globules (II)—the **spermatoblasts** (*v. Ebner*); these consist of soft finely granular protoplasm, and usually have an oval nucleus in their lower part. During development, each lobule of the spermatoblast elongates into a tail (IV, *r*), while the deeper part forms the head and middle pieces of the future spermatozoon (IV, *k*). At this stage the spermatoblast is like a greatly enlarged, irregular, cylindrical epithelial cell. When development is complete, the head and middle pieces are detached (III, *t*), and ultimately the remaining part of the spermatoblast undergoes fatty degeneration. Not unfrequently in spermatozoa we may observe a small mass of protoplasm adhering to the tail and the middle piece (III, *t*). Between the spermatoblasts are numerous round amœboid cells devoid of an en-

velope, and connected to each other by processes. They seem to secrete the *fluid* part of the semen, and they may therefore be called **seminal cells** (I, *s*, II, III, IV, *p*). A spermatozoon, therefore, is a detached independently mobile cilium of an enlarged epithelial cell. Some observers adhere to the view that the spermatozoa are, in part at least, formed within round cells, by a process of endogenous development.

[All observers are agreed that the appearance of a seminal tubule differs according to the state of activity of the cells lining it, but in the case of a tubule with developing spermatozoa, although the appearance seen in transverse section of a tubule is on the whole such as is shown in fig. 776, I, still the view stated above is not the one which has the largest number of supporters. Other observers interpret the appearances differently. According to the other view, there is but one kind of gland-cell lining the tubules, and certain of these cells or **spermatogonia**—lying next the periphery—by successive acts of division give rise to round cells with dark nuclei, *i.e.*, to daughter cells or **spermatocytes**, which arrange themselves radially towards the lumen of the tubule. They are represented by the indifferent cells lying between the so-called spermatoblasts in fig. 776, I.

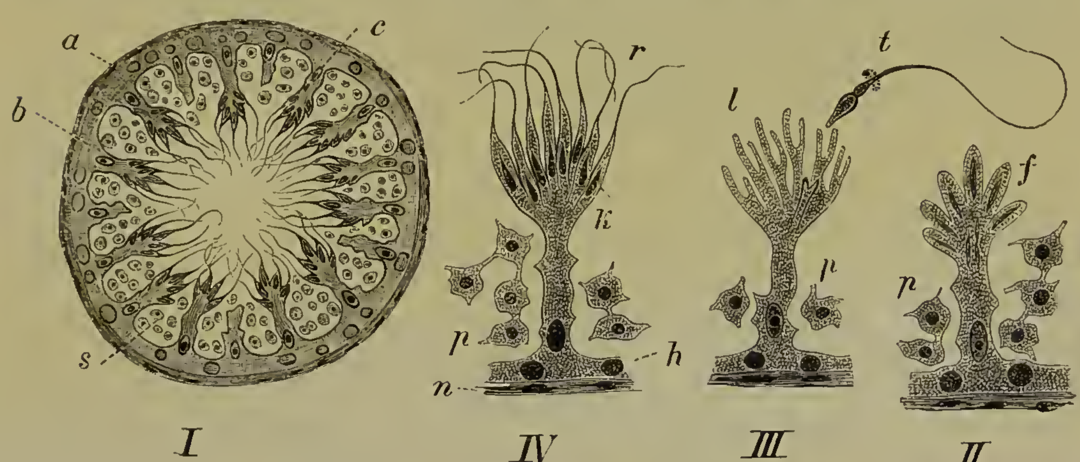


Fig. 776.

Semi-diagrammatic spermatogenesis: I, transverse section of a seminal tubule—*a*, membrane; *b*, protoplasmic inner lining; *c*, spermatoblast; *s*, seminal cells. II, Unripe spermatoblast —*f*, rounded clavate lobules; *p*, seminal cells. IV, spermatoblast, with ripe spermatozoa (*k*) not yet detached; tail, *r*; *n*, wall of the seminal tubule; *h*, its protoplasmic layer. III, spermatoblast with a spermatozoon free, *t*.

The last generation of cells derived from these spermatocytes, lying next the lumen of the tube, are called **spermatides**, and these last become the spermatozoa; in the process the nucleus of each spermatide becomes the head, a small part of the protoplasm becomes the tail of the spermatozoa. The largest part of the protoplasm of the spermatide remains, and these residues, as it were, come together and form the large branched structure, which on the previously stated view were called spermatoblasts. The young spermatozoa lie embedded in the tops of these masses of protoplasm, thus an entirely different explanation is given of the appearances seen in a seminal tubule].

According to Benda and v. Ebner, the spermatoblasts are formed by the coalescence (copulation) of a group of seminal cells with the lower part of the foot-plate and stalk of the spermatoblasts. Each seminal cell forms from its nucleus the head, and from its protoplasm the tail of a spermatozoon. For the complete formation of these parts, there must be a coalescence of the seminal cells with the spermatoblasts.

Shape of Spermatozoa.—The spermatozoa of most animals are like cilia with larger or smaller heads. The head is elliptical (mammals), or pear-shaped (mammals), or cylindrical (birds, amphibians, fish), or cork-screw (singing birds, paludina), or merely like hairs (insects—fig. 775).

Immobile seminal cells, quite different from the ordinary forms, occur in myriapoda and the oyster.

433. THE OVARY—OVUM—UTERUS.—[**Structure of the Ovary.**—The ovary consists of a connective-tissue **framework**, with blood-vessels, nerves, lymphatics, and numerous non-striped muscular fibres. The **ova** are embedded in this matrix (fig. 777). The surface of the ovary is covered with a layer of columnar epithelium (fig. 778, *e*), the remains of the **germ-epithelium**. The most superficial layer is called the **albuginea**; it does not contain any ova. Below it is the **cortical layer** of Schrön, which contains the smallest Graafian follicles ($\frac{1}{100}$ inch—fig. 777), while deeper down are the larger follicles ($\frac{1}{30}$ to $\frac{1}{100}$ inch). There are 40,000 to 70,000 follicles in the ovary of a female infant. Each ovum lies within its follicle or **Graafian vesicle.**]

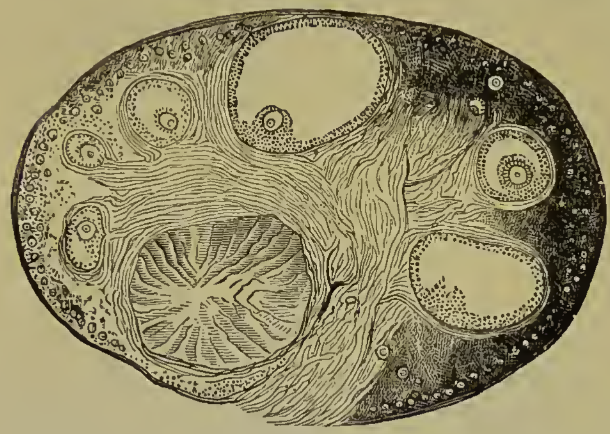


Fig. 777.

Section of a cat's ovary. The place of attachment or hilum is below. On the left is a corpus luteum.

Structure of an Ovum.—The human ovum (*C. E. v. Baer*, 1827) is 0·18 to 0·2 mm. [$\frac{1}{120}$ in.] in diameter, and is a spherical cellular body with a thick, solid, elastic envelope, the **zona pellucida**, with radiating striæ (fig. 779). The zona pellucida encloses the cell-contents represented by the protoplasmic, granular, contractile **vitellus** or **yelk**, which in turn contains the eccentrically placed spherical nucleus or **germinal vesicle** (40–50 μ—*Purkinje*, 1825; *Coste*, 1834). The germinal vesicle contains the nucleolus or **germinal spot** (5–7 μ—*R. Wagner*, 1835). The *chemical composition* is given in § 232.

[**Ovum.**		**Cell.**
Zona pellucida	corresponds to the	Cell-wall.
Vitellus	,, ,,	Cell-contents.
Germinal vesicle	,, ,,	Nucleus.
Germinal spot	,, ,,	Nucleolus.]

[This arrangement shows the corresponding parts in a cell and the ovum, and in fact the **ovum** represents a **typical cell.**]

The **zona pellucida** (figs. 779, 780, V, Z), to which cells the Graafian follicles are often adherent, is a cuticular membrane formed secondarily by the follicle (*Pflüger*). According to Van Beneden, it is lined by a thin membrane next the vitellus, and he regards the thin membrane as the original cell-membrane of the ovum. The fine radiating striæ in the zona are said to be due to the existence of numerous canals (*Kölliker, v. Sehlen*). It is still undecided whether there is a special **micropyle** or hole for the entrance of the spermatozoa.

A **micropyle** has been observed in some ova (holothurians, many fishes, mussels). The ova of some animals (many insects, *e.g.*, the flea) have porous canals in some part of their zona, and these serve both for the entrance of the spermatozoa and for the respiratory exchanges in the ovum.

The development of the ova takes place in the following manner:—The surface of the ovary is covered with a layer of cylindrical epithelium—the so-called "**germ-epithelium**"—and between these cells lie somewhat spherical "**primordial ova**" (fig. 780, I, *a*, *a*). The epithelium covering the surface dips into the ovary at various places to form "**ovarian tubes**" (fig. 780). These tubes, from and in which the ova are developed (*Waldeyer*), become deeper and deeper, and they contain, in their interior, large single spherical cells with a nucleus and a nucleolus,

and other smaller and more numerous cells lining the tube. The large cells are the cells (**primordial ova**) that are to develop into ova, while the smaller cells are the epithelium of the tube, and are direct continuations of the cylindrical epithelium on the surface of the ovary. The upper extremities of the tubes become closed, while the tube itself is divided into a number of rounded compartments — cut off, as it were, by the ingrowth of the ovarian stroma (I, *c*,). Each compartment so cut off usually contains one, or at most two, ova (IV, *o*, *o*), and becomes developed into a Graafian follicle. The embryonic follicle enlarges, and fluid appears within it; while its lateral small cells become changed into the epithelium lining the Graafian follicle itself, or those of the membrana granulosa. The cells of the membrana granulosa form an elevation at one part—the **discus proligerus**—by which the ovum is attached to the membrana granulosa. The follicles are at first only 0·03 mm. in diameter, but they become larger, especially at puberty. [The smaller ova are near the surface of the ovary, the larger ones deeper in its substance (fig. 778).] When a Graafian follicle with its ovum is about to **ripen** (IV), it sinks or passes downwards into the substance of the ovary, and enlarges at the same time by the accumulation of fluid—the **liquor folliculi** — between the tunica and membrana granulosa. It is covered by a vascular outer membrane—the **theca folliculi** —which is lined by the epithelium constituting the **membrana granulosa** (IV, *g*). When a **Graafian follicle** is about to **burst**, it again rises to the surface of the ovary, and attains a diameter of 1·0 to 1·5 mm., and is now ready to burst and discharge its ovum. [The tissue between the enlarged Graafian

Fig. 778.

Section of an ovary. *c*, germ-epithelium ; 1, large-sized follicles ; 2, 2, middle-sized, and 3, 3, smaller-sized follicles ; *o*, ovum within a Graafian follicle ; *v*,*v*, blood-vessels of the stroma ; *g*, cells of the membrana granulosa.

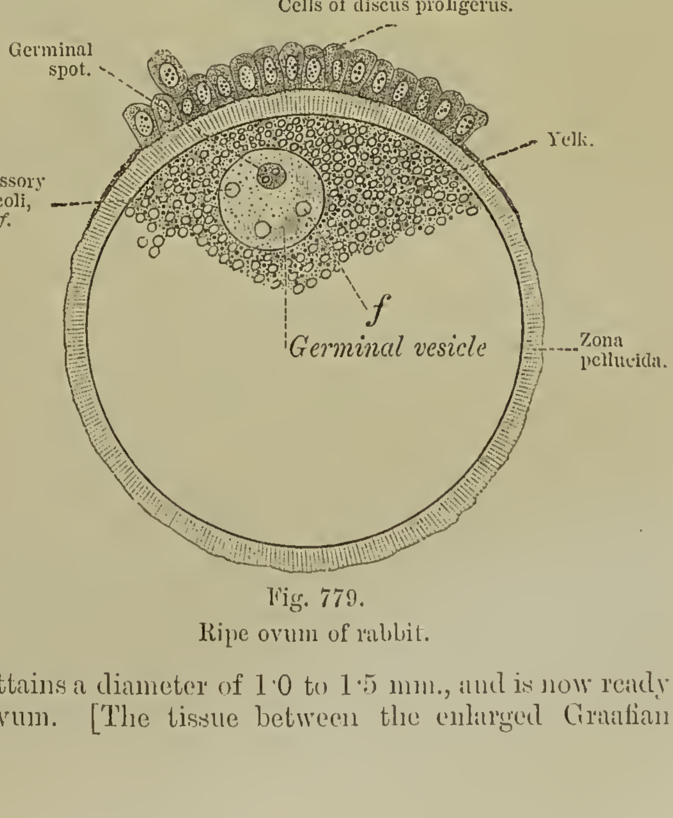


Fig. 779.

Ripe ovum of rabbit.

follicle and the surface of the ovary gradually becomes thinner and thinner and less vascular, and at last gives way, when the ovum is discharged and caught by the fimbriated extremity of the Fallopian tube embracing the ovary, so that the ovum is shed into the Fallopian tube itself.] Only a small number of the Graafian follicles undergo development normally, by far the greatest number atrophy and never ripen. (The study of the development of the ova and ovary was advanced particularly by Martin Barry, Pflüger, Billroth, Schrön, His, Waldeyer, Kölliker, Koster, Lindgren, Schulin, Foulis, Balfour, and others.)

According to Waldeyer, the mammalian ovum is not a simple cell, but a compound structure. The original primitive ovum is, according to him, formed only of the germinal vesicle and germinal spot, with the surrounding membranous clear part of the vitellus (fig. 780, III). The remainder of the vitellus is developed by the transformation of granulosa cells, which also form the zona pellucida.

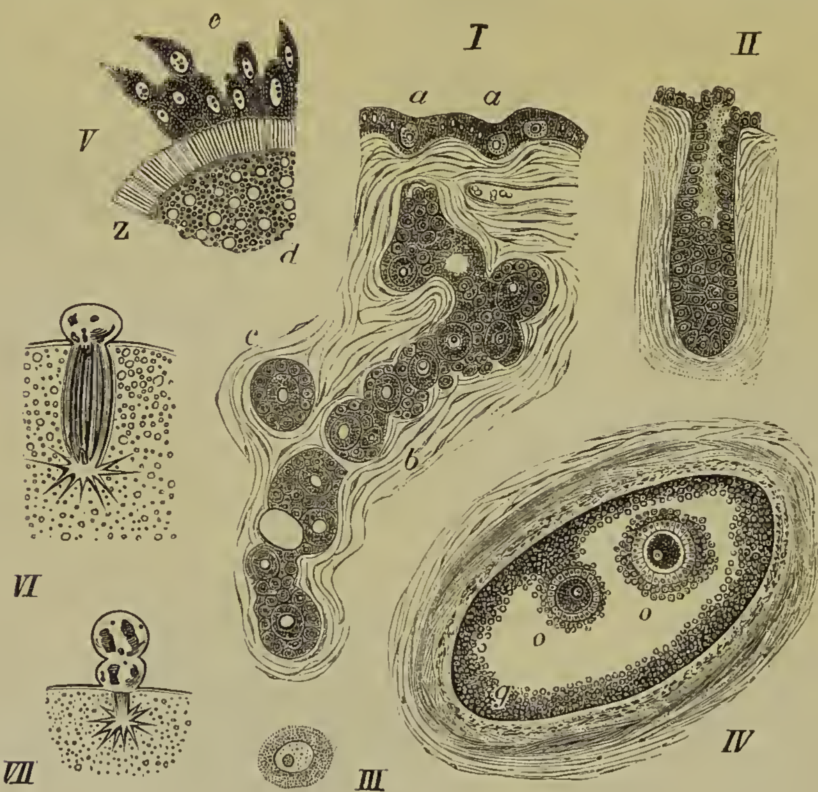


Fig. 780.

I, An ovarian tube in process of development (new-born girl). *a*, *a*, young ova between the epithelial cells on the surface of the ovary; *b*, the ovarian tube with ova and epithelial cells; *c*, a small follicle cut off and enclosing an ovum. II, Open ovarian tube from a bitch. III, Isolated primordial ovum (human). IV, Older follicle with two ova (*o*, *o*) and the tunica granulosa (*g*) of a bitch. V, Part of the surface of a ripe ovum of a rabbit —*z*, zona pellucida; *d*, vitellus; *e*, adherent cells of the membrana granulosa. VI, First polar globule formed. VII, Formation of the second polar globule (*Fol*).

Holoblastic and Meroblastic Ova.—The ova of frogs and cyclostomata have the same type as mammalian ova; they are called **holoblastic ova**, because all their contents go to form cells which take part in the formation of the embryo. In contrast with these, the birds, the monotremes alone amongst the mammals (*Caldwell*), the reptiles and the other fishes have **meroblastic ova** (*Reichert*). The latter, in addition to the white or formative yelk, which corresponds to the yelk of the holoblastic eggs, and gives rise to the embryonic cells, contains the food-yelk (yellow in birds), which during development is a reserve store of food for the developing embryo.

Hen's Egg.—The small, white, round, finely granular speck, the **cicatricula**,

blastoderm, or **tread**, which is 2·5–3·5 mm. broad and 0·28–0·37 thick, lying upon the surface of the yellow yelk, corresponds to the contents of the mammalian ovum, and is, therefore, the formative yelk. In the cicatricula lie the germinal vesicle and spot (figs. 780, 783). From the tread, in which lie the characteristic white yelk elements, processes pass into the yellow yelk. A part passes as an exceed-

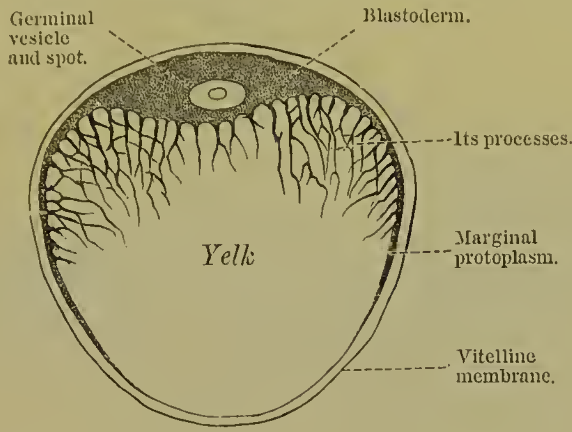


Fig. 781.
Scheme of a meroblastic egg.

Fig. 782.
a, White ; *b*, yellow yelk granules.

ingly thin layer round the yelk, or cortical protoplasm. [The cicatricula in an unincubated egg is always uppermost whatever the position of the egg, provided the contents can rotate freely, and this is due to the lighter specific gravity of that part of the yelk in connection with the cicatricula (fig. 783). In a fecundated egg the cicatricula has a white margin (the **area opaca**), surrounding a clear transparent area, the beginning of the **area pellucida**, containing an opaque spot in its centre. If an egg be boiled very hard, and a section made of the yelk, it will be found to consist of alternating layers of white and yellow yelk. The outermost layer is a thin layer of white yelk, which is slightly thicker at the margin of the cicatricula. Within the centre of the yelk is a flask-shaped mass of white yelk, the neck of the flask being connected with the white yelk outside. This flask-shaped mass does not become so hard on being boiled, and its upper expanded end is known as the "**nucleus of Pander**" (fig. 783). The great mass of the yelk is made up, however, of yellow yelk.

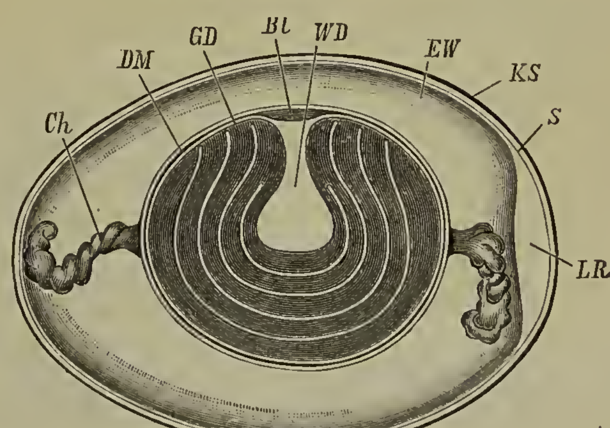


Fig. 783.
Diagrammatic longitudinal section through an unincubated hen's egg. *Bl*, blastoderm ; *GD*, yellow yelk ; *WD*, white yelk and nucleus of Pander ; *DM*, vitelline membrane ; *EW*, "white" ; *Ch*, chalazae ; *S*, shell membrane ; *KS*, shell ; *LR*, air-chamber.

Microscopically, the **yellow yelk** consists of soft yellow spheres, of from 23–100 μ in diameter, and they are often polyhedral from mutual pressure (fig. 782, *b*). [They are very delicate and non-nucleated, but filled with fine granules, which are, perhaps, proteid in their nature, as they are insoluble in ether and alcohol. They are developed by the proliferation of the granulosa cells of the Graafian follicle, which also seem ultimately to form the granulo-fibrous double envelope or the **vitelline membrane** (*Eimer*). The whole yelk of the hen's egg is

regarded by some observers as equivalent to the mammalian ovum *plus* the corpus luteum. Microscopically, the **white yelk** consists of small vesicles (5–75 μ) containing a refractive substance and larger spheres containing several smaller spherules (fig. 782, *a*). The whole yelk is enveloped by the **vitelline membrane**, which is transparent, but possesses a fine fibrous structure, and it seems to be allied to elastic tissue.]

When the yelk is fully developed within the Graafian follicles of the hen's ovarium, the follicle bursts and discharges the yelk, which passes into the oviduct, where in its passage it rotates, owing to the direction of the folds of the mucous membrane of the oviduct. The numerous glands of the oviduct secrete the **albumin**, or white of the egg, which is deposited in layers around the yelk in its passage along the duct, and forms at the anterior and posterior **chalazae**. [The **chalazae** are two twisted cords composed of twisted layers of the outer denser part of the albumin. They extend from the poles of the yelk not quite to the outer part of the albumin (fig. 783, *Ch*). [The albumin is invested by the **membrana testacea** or **shell-membrane**, which is composed of two layers—an outer thicker and an inner thinner one (fig. 783). Over the greater part of the albumin these two layers are united, but at the broad end of the hen's egg they tend to separate, and air passing through the porous shell separates them more and more as the fluid of the egg evaporates. This air-space is not found in fresh-laid eggs.] The layers consist of spontaneously coagulated kera-tin-like fibres arranged in a spiral manner around the albumin (*Lindvall and Hammarsten*). [External to this is the **test** or **shell**, which consists of an organic matrix impregnated with lime salts.] The shell consists of albumin impregnated with lime salts, which form a very porous mortar. [The shell is porous, and its inner layer is perforated by vertical canals, through which the respiratory exchange of the gases can take place.] In the eggs of some birds there is an outer structureless, porous, slimy, or fatty cuticula. The shell is secreted in the lower part of the oviduct. The shell is partly used up for the development of the bones of the chick (*Prout, Gruwe*), although this is denied by *Polt and Preyer*. The pigment which often occurs in many layers of the surface of the eggs of some birds appears to be a derivative of hæmoglobin and biliverdin.

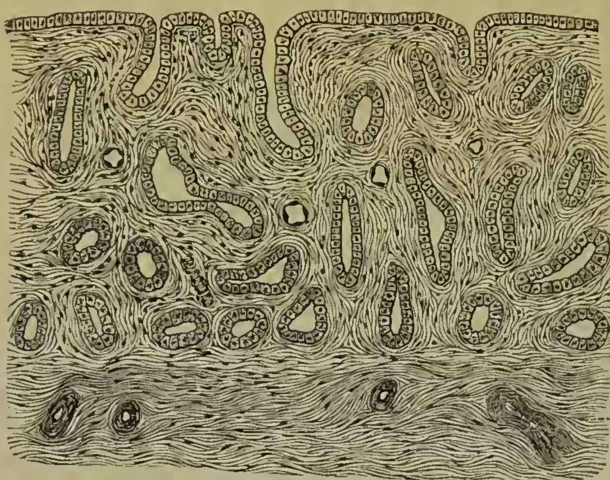


Fig. 784.
Vertical section of the normal uterine mucous membrane, *m*, together with a part of the subjacent muscular layer, m_1.

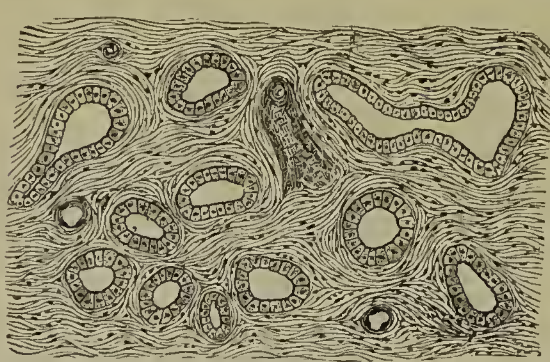


Fig. 785.
Surface section of fig. 784.

Chemical Composition.—The **yellow yelk** is alkaline, and coloured yellow owing to the presence of **lutein**, which contains iron. It contains several proteids [including a globulin body called **vitellin** (p. 465)], a body resembling nuclein, lecithin, vitellin, glycerin-phosphoric acid, cholesterin, olein, palmitin, dextrose, potassic chloride, iron, earthy phosphates, fluoric and silicic acids. The presence of cerebrin, glycogen, and starch is uncertain. [Dareste states that starch is present.]

[The **albumin** of **egg** contains—water, 86 per cent.; proteids, 12; fat and extractives, 1·5; saline matter, including sodic and potassic chlorides, phosphates, and sulphates, ·5 per cent.]

[The **uterus**, a thick hollow muscular organ, is covered externally by a **serous coat**, and lined internally by a **mucous membrane**, while between the two is the

thick **muscular coat**, composed of smooth muscular fibres arranged in a great number of layers and in different directions. The mucous membrane of the body of the uterus in the unimpregnated condition has no folds, while the muscularis

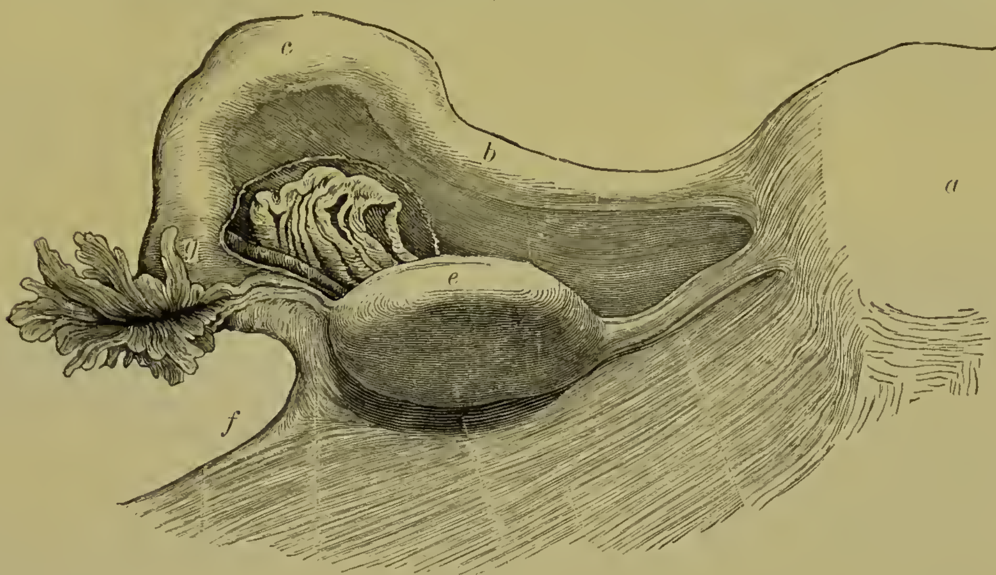


Fig. 786.

Left broad ligament, Fallopian tube, ovary, and parovarium. *a*, uterus; *b*, isthmus of Fallopian tube; *c*, ampulla; *g*, fimbriated end of the tube, with the parovarium to its right; *e*, ovary; *f*, ovarian ligament.

mucosæ is very well developed, and forms a great part of the uterine muscular wall. The mucous membrane is lined by a single layer of columnar ciliated epithelium. A vertical section shows the mucous membrane to contain numerous tubular glands (fig. 784)—the **uterine glands**—which branch towards their lower ends. They have a membrana propria, and are lined by a single layer of ciliated epithelium, a small lumen being left in the centre. The utricular glands are not formed during intra-uterine life (*Turner*), nor are there any glands in the human uterus at birth (*G. J. Engelmann*). There are numerous slit-like *lymphatic* spaces in the mucous membrane (*Leopold*), which communicate with well-marked lymphatic vessels existing in this and the other layers of the organ. In the **cervix**, the mucous membrane is folded, representing in the virgin the appearance known as the arbor vitæ. The external surface of the vaginal part of the neck is covered by stratified squamous epithelium, like the vagina.]

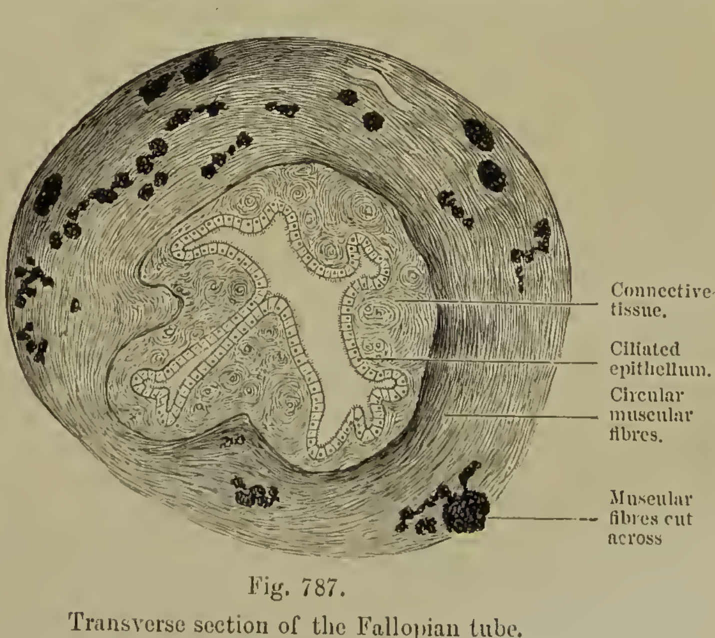


Fig. 787.

Transverse section of the Fallopian tube.

[The **Fallopian tubes** are really the ducts of the ovaries (fig. 786). They consist of a serous, muscular (an external, longitudinal, and an internal circular) layer of non-striped muscle, and a mucous layer thrown into many folds and lined by a single layer of ciliated columnar epithelium, but no glands (fig. 787).]

434. PUBERTY.—The term **puberty** is applied to the period at which a human being becomes capable of procreating, which occurs from the 13th to 15th years in the female, and the 14th to 16th in the male. In warm climates, puberty may occur in girls even at 8 years of age. Towards the 40th to 50th year, the procreative faculty ceases in the female with the cessation of the menses; this constitutes the **menopause** or **grand climacteric**, whilst in man the formation of seminal fluid has been observed up to old age. From the period of puberty onwards, the sexual appetite occurs, and the ripe ova are discharged from the ovary. [But ova are discharged even before puberty or menstruation has occurred.] At puberty, the internal and external generative organs and their annexes become more vascular and undergo development; the pelvis of the female assumes the characteristic female shape. For the changes in the mammæ see § 330. At the same time hair is developed on the pubes and axilla, and in the male on the face, while the sebaceous glands become larger and more active.

Other changes occur, especially in the **larynx**. In the boy the larynx elongates in its antero-posterior diameter, the thyroid, or Adam's apple, becomes more prominent, while the vocal cords lengthen, so that the voice is hoarse, or husky, or "breaks," the voice being lowered at least an octave. In the female the larnyx becomes longer, while the compass of the voice is increased. The vital capacity (§ 108), corresponding to the increase in the size of the chest, undergoes a considerable increase; the whole form and expression assume the characteristic sexual appearance, while the psychical energies also receive an impulse.

435. MENSTRUATION.—External Signs.—At regular intervals of time, of $27\frac{1}{3}$–28 days in a mature female, there is a rupture of one or more ripe Graafian follicles, while at the same time there is a discharge of blood from the external genitals. This is known as the process of *menstruation* (or menses, catamenia, or periods). Most women menstruate during the first quarter of the moon, and only a few at new and full moon (*Strohl*). In mammals, the analogous condition is spoken of as the period of heat [or the "rut" in deer]. There is a slightly bloody discharge from the external genitals in carnivora, the mare, and cow (*Aristotle*), while apes in their wild condition have a well-marked menstrual discharge (*Neubert*). [Observations on cases where abdominal section has been performed have shown that the Graafian follicles mature and burst at any time (*Lawson Tait*, *Leopold*).]

The **onset** of menstruation is usually heralded by constitutional and local phenomenon—there is an increased feeling of congestion in the internal generative organs, pain in the back and loins, tension in the region of the uterus and ovaries, which are sensitive to pressure, fatigue in the limbs, alternate feeling of heat and cold, and even a slight increase of the temperature of the skin (*Kersch*). There may be retardation of the process of digestion and variations in the evacuation of the fæces and urine, and in the secretion of sweat. The discharge is *slimy* at first, and then becomes *bloody*, lasting three to four days; the blood is venous, and shows little tendency to coagulate, provided it is mixed with much alkaline mucus from the genital passages; but, if the hæmorrhage be free, the blood may be clotted. The **quantity** of blood is 100 to 200 grms. [The blood contains many white blood-corpuscles and epithelial cells.] After cessation of the discharge of blood there is a moderate amount of mucus given off.

The characteristic internal phenomena which accompany menstruation are:—(1) The changes in the uterine mucous membrane; and (2) the rupture of the Graafian follicle.

1. **Changes in the uterine mucous membrane.**—The uterine mucous membrane is the chief source of the blood. The ciliated epithelium of the congested, swollen, and folded, soft, thick (3 to 6 mm.) mucous membrane is shed. The orifices of the numerous mucous glands of the mucous membrane are distinct, the glands

enlarge, and the cells undergo *fatty degeneration*, and so do the tissue and the blood-vessels lying between the glands. The tissue contains more leucocytes than normal. This fatty degeneration and the excretion of the degenerated tissue occur, however, only in the superficial layers of the mucosa, whose blood-vessels, when torn across, yield the blood. The deeper layers remain intact, and from them, after menstruation is over, the new mucous membrane is developed (*Kundrat and G. J. Engelmann*). [Leopold denies the existence of this fatty degeneration. According to Williams, the entire mucous membrane is removed at each menstrual period, and it is regenerated from the muscular coat (fig. 789). The mucous membrane of the cervix remains free from these changes.]

Fig. 788. Fig. 789.

Fig. 788.—Diagram of the uterus just before menstruation. The shaded portion represents the mucous membrane. Fig. 789.—Uterus when menstruation has just ceased, showing the cavity of the body deprived of mucous membrane (*J. Williams*).

2. **Ovulation.**—The second important internal phenomenon is *ovulation*, in which process the ovary becomes more vascular—the ripe follicle is turgid with fluid, and in part projects above the surface of the ovary. The follicle ultimately bursts, its membranes and the epithelium covering of the ovary are torn or give way under the pressure, the bursting being accompanied by the discharge of a small amount of blood. At the same time, the congested, turgid, and erected fimbriated extremity of the Fallopian tube is applied to the ovary, so that the discharged ovum, with its adherent granulosa cells, and the liquor folliculi, are caught by the funnel-shaped extremity of the tube (fig. 786). The ovum, when discharged, is carried towards the uterus by the ciliated epithelium (§ 433) of the tube, and perhaps also partly by the contraction of its muscular coat. Ducallicz and Küss found that, by fully injecting the blood-vessels, they could imitate the erection of the Fallopian tube. Rougat points out that the non-striped muscle of the broad ligaments may cause constriction of the vessels, and thus secure the necessary injection of the blood-vessels of the Fallopian tube.

Pflüger's Theory of Ovulation.—There are two theories as to the connection between ovulation or the discharge of an ovum and the escape of blood from the uterine mucous membrane. Pflüger regards the bloody discharge from the superficial layers of the uterine mucous membrane as a physiological preparation or "freshening" of the tissue (in the surgical sense), by which it will be prepared to receive the ovum when the latter reaches the uterus, so that union can take place between the ovum and the freshly-exposed surface of the mucous membrane, and thus the ovum will receive nourishment from a new surface.

Reichert's Theory.—This view is opposed to that of Reichert, Engelmann, Williams, and others. According to Reichert's theory, before an ovum is discharged at all there is a sympathetic change in the uterine mucous membrane, whereby it becomes more vascular, more spongy, and swollen up. The mucous membrane so altered is spoken of as the *membrana decidua menstrualis*, and from its nature it is in a proper condition to receive, retain, and nourish a fertilised ovum which may come into contact with it. If the ovum, however, be not fertilised, and escape from the genital passages, then the uterine mucous membrane degenerates, and blood is shed as above described. According to this view the hæmorrhage from the uterine mucous membrane is a sign of the non-occurrence of pregnancy; the mucous membrane degenerates because it is not required for this occasion; the menstrual blood is an external sign that the ovum has not been impregnated. So that pregnancy, *i.e.*, the development of the

embryo in utero, is to be calculated, not from the last menstruation, but from some time between the last menstruation and the period which does not occur.

In some cases the ovulation and the formation of the decidua menstrualis occur separately, so that there may be menstruation without ovulation, and ovulation without menstruation.

Corpus Luteum.—When a Graafian follicle bursts, it discharges its contents and collapses; in the interior are the remains of the membrana granulosa and a small effusion of blood, which soon coagulates. The small rupture soon heals, after the serum is absorbed. The vascular wall of the follicle swells up. Villous prolongations or granulations of young connective-tissue, rich in capillaries and cells, grow into the interior of the follicle (fig. 791). Colourless blood-corpuscles also wander into the interior. At the same time the cells of the granulosa proliferate, and form several layers of cells, which ultimately, after the disappearance of a number of blood-vessels, undergo fatty degeneration, **lutein** and *fatty* matter being formed, and it is this mass which gives the corpus luteum its yellow colour (fig. 792). The capsule becomes more and more fused with the ovarian stroma. If pregnancy does not take place after the menstruation, then the fatty matter is rapidly absorbed, and the effused blood is changed into hæmatoidin (§ 20) and other derivatives of hæmoglobin, while there is a gradual shrivelling of the whole mass, which is complete in about four weeks, only a very small remainder being left. Such a corpus luteum, *i.e.*, one not accompanied by pregnancy, is called a **false corpus luteum.** If, however, pregnancy occurs, then the corpus luteum, instead of shrivelling, grows and becomes a large body, especially at the third and fourth month, the walls are thicker, the colour deeper, so that the corpus luteum at the period of delivery may be 6 to 10 mm. in diameter, and its remains may be found in the ovary for a very long time thereafter (fig. 791).

Fig. 790.
Fresh corpus luteum.

Fig. 791.
Corpus luteum of cow ($\times 1\frac{1}{2}$).

Fig. 792.
Lutein cells from the corpus luteum of cow.

This form is sometimes spoken of as a **true corpus luteum.** [We cannot draw a sharp distinction between these two forms.] Only a very small number of the ova in the ovary undergo development and are discharged; by far the greater number degenerate (*Slavjansky*).

436. PENIS—ERECTION.—Penis.—[The penis is composed of the two long cylindrical **corpora cavernosa**, and the **corpus spongiosum**, which lies between and below them, and surrounds the urethra (fig. 793); these are held together by fibrous and muscular sheaths, and are com-

posed of erectile tissue.] Our knowledge of the distribution of the blood within the penis is chiefly due to C. Langer's researches. The albuginea of the corpus spongiosum consists of tendinous connective-tissue, containing thickly-woven elastic tissue and smooth muscular fibres, which together form a solid fibrous envelope, from which numerous interlacing trabeculæ pass into the interior, so that the corpus spongiosum comes to resemble a sponge. The anastomosing spaces bounded by these trabeculæ form a series of intercommunicating venous spaces or sinuses filled with blood and lined by a layer of endothelium constituting **erectile tissue** (fig. 794). The largest sinuses lie in the lower and external part of the corpus cavernosum, while they are less numerous and smaller in the upper part. The small **arteries** arise from the A. profunda penis, which runs along the septum, and pass to the trabeculæ after following a very sinuous course. At the outer part of the corpus spongiosum, some of the small arteries become directly continuous with the larger venous sinuses; some of them, however, terminate in capillaries both in the outer part and within the corpus spongiosum, the *capillaries* ultimately terminating in the venous sinuses. The helicine arteries of the penis described by Joh. Müller are merely much twisted arteries. The *deep veins* of the penis arise by fine veinlets within the body of the organ, while the veins proceeding from the cavernous spaces pass to the dorsum of the penis to form the *vena dorsalis penis* (fig. 793). As these vessels have to traverse the meshes of the vascular network in the cortex of the corpora cavernosa penis, it is evident that, when the network is congested by being filled with blood, it must compress the outgoing venous trunks. The corpus cavernosum urethræ consists for the most part of an external layer of closely packed anastomosing veins, which surround the longitudinally directed blood-vessels of the urethra.

Fig. 793.

Transverse section across the middle third of the body of the penis. *n*, nerve; *a*, artery; *v*, vein.

In the dog, all the arteries of the penis run at first towards the surface, where they divide into penicilli. The veins arise from the capillary loops in the papillæ, and they empty their blood into the cavernous spaces. Only a small part of the blood passes to the cavernous spaces through the internal capillaries and veins, but arterial blood never flows directly into these spaces (*M. v. Frey*).

Mechanism of Erection.—Erection is due to the overfilling of the blood-vessels of the penis with blood, whereby the volume of the organ is increased four or five times, while, at the same time, there are also a higher temperature, increased blood-pressure (to $\frac{1}{6}$ of that in the carotid—*Eckhard*), with at first a pulsatile movement, increased consistence, and erection of the organ.

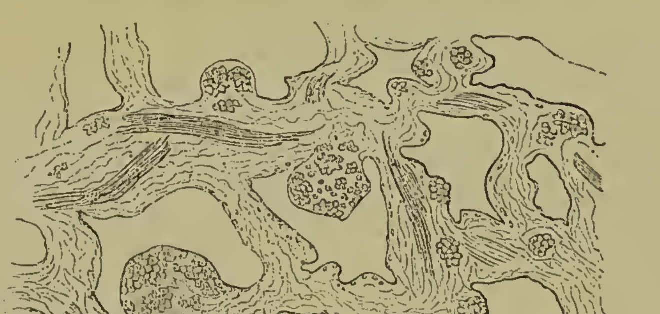


Fig. 794.

Erectile tissue. *a*, trabeculæ of connective-tissue with elastic fibres and smooth muscle (*c*); *b*, venous spaces.

Regner de Graaf obtained complete erection of the penis by forcibly injecting its blood-vessels (1668).

The **preliminary phenomena** consist in a considerable increase of the arterial blood-supply, the arteries being dilated and pulsating strongly. The arteries are

controlled by the nervi erigentes. The **nervi erigentes** [called by Gaskell the **pelvic splanchnics** (fig. 530) arise chiefly from the second (more rarely the third) sacral nerves (dog), and have ganglionic cells in their course (*Lovén, Nikolsky*). These nerves contain **vaso-dilator fibres**, which can be excited in part reflexly from the sensory nerves of the penis, the transference centre being in the centre for erection in the spinal cord (§ 372, 4). Sensory impressions produced by voluntary movements of the genital apparatus (by the ischio- and bulbo-cavernosi and cremaster muscles) can also discharge this reflex; while the thought of sexual impulses, referable to the penis, tends to induce erection. The nervi erigentes also supply the longitudinal fibres of the rectum (*Fellner*).

The **centre for erection** in the spinal cord (§ 362, 2) is, however, controlled by the dominating vaso-dilator centre in the medulla oblongata (§ 372), and the two centres are connected by fibres within the cord; hence stimulation of the upper part of the cord, as by asphyxiated blood (§ 362, 5) or muscarin, may also be followed by erection (*Nikolsky*). [The seminal fluid is frequently found discharged in persons who have been hanged.]

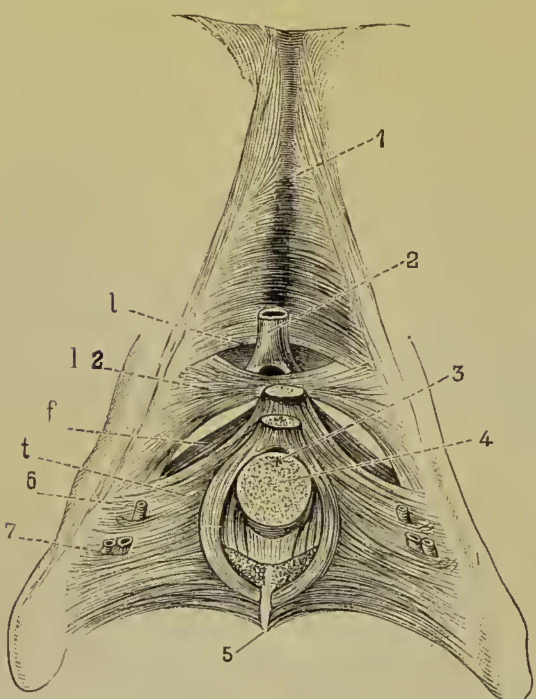


Fig. 795.

Anterior wall of the pelvis with the urogenital septum seen from the front. The corpus cavernosum (4) with the urethra (3) is cut across below its exit from the pelvis. 1, symphysis pubis; 2, dorsal vein of the penis; 5, part of the bulbo-cavernosus; *t*, deep transversus perinei with its fascia (*f*); 6, vena profunda penis; 7, artery and vein of the bulbo-cavernosus.

The *psychical activity of the cerebrum* has a decided influence on the genital vaso-dilator nerves. Just as the psychical disturbance which accompanies anger or shame is followed by dilatation of the blood-vessels of the head, owing to stimulation of the vaso-dilator fibres, so when the attention is directed to the sexual centres there is an action upon the nervi erigentes. This action of the brain is more comprehensible, since we know that the diameter of the blood-vessels is affected by the cortex cerebri (§ 377). The fibres probably pass from the cerebrum through the peduncles of the cerebrum and the pons; as a matter of fact, if these parts be stimulated, erection may take place (§ 362, 4) (*Eckhard*).

When the impulse to erection is obtained by the increased supply of arterial blood, the *full completion* of the act is brought about by the activity of the following transversely striped **muscles**:—(1) The *ischio-cavernosus* arises from the coccyx, and by its tendinous union surrounds the root of the penis (fig. 203). When it contracts, it compresses the root of the penis from above and laterally, so that the outflow of blood from the penis is hindered. It has no action on the dorsal vein of the penis, as this vessel lies in a groove on the dorsum of the penis, and is therefore protected from compression by the tendon. (2) The *deep transversus perinei* is perforated by the venæ profundæ penis, which come from the corpora cavernosa, so that when it contracts it must compress these veins between the tense horizontal fibres (fig. 795, 6). The deep veins of the penis join the common pudendal vein and the plexus Santorini. (3) Lastly, the *bulbo-cavernosus* is con-

cerned in the hardening of the urethral corpus spongiosum, as it compresses the bulb of the urethra (figs. 795, 5, 203). All these muscles are partly under the control of the will, whereby the erection may be increased. Normally, however, their contraction is excited **reflexly** by stimulation of the sensory nerves of the penis (§ 362, 4).

The congestion of blood is not complete, else, in pathological cases, continuous erection, as in satyriasis, would give rise to gangrene. The accumulation of the blood in the penis is favoured by the fact that the origins of the veins of the penis lie in the corpus cavernosum, which, when it enlarges, must compress them. There are also trabecular smooth muscular fibres, which compress the large venous plexus of Santorini.

That erection is a complex motor act depending on the nervous system, is proved by an experiment of Hausmann, who found that section of the nerves of the penis prevented erection in a stallion. The imperfect erection which occurs in the female is confined to the corpora cavernosa clitoridis and the bulbi vestibuli. During erection, the passage from the urethra to the bladder is closed, partly by the swelling of the caput gallinaginis, and partly by the action of the sphincter urethræ, which is connected with the deep transversus perinei.

437. EMISSION AND RECEPTION OF THE SEMEN.—In connection with the **emission** of the seminal fluid, we must distinguish two different factors—(1) its passage from the testicles to the vesiculæ seminales; (2) the act of emission itself. The former is caused by the newly secreted fluid forcing on that in front of it, by the action of the ciliated epithelium (which lines the epididymis to the beginning of the vas deferens), and also by the peristaltic movements of the smooth muscular fibres of the vas deferens. Emission, however, requires strong peristaltic contractions of the vasa deferentia and the vesiculæ seminales, which are brought about by the reflex stimulation of the emission centre in the spinal cord (§ 362, 5). As soon as the seminal fluid reaches the urethra, there is a rhythmical contraction of the bulbo-cavernosus muscle (produced by the mechanical dilatation of the urethra), whereby the fluid is forcibly ejected from the urethra. Both vasa deferentia and vesiculæ do not always eject their contents into the urethra simultaneously. With moderate excitement the contents of only one may be discharged. The ischio-cavernosus and deep transversus perinei contract at the same time as the bulbo-cavernosus, although the former have no effect on the act of ejaculation. In the female also, under normal circumstances, at the height of the sexual excitement there is a reflex movement corresponding to emission. It consists of a movement analogous to that in man. At first there is a reflex peristaltic movement of the Fallopian tube and uterus, proceeding from the end of the tube towards the vagina, and produced reflexly by the stimulation of the genital nerves.

Dembo observed that stimulation of the anterior upper wall of the vagina in animals caused a gradual contraction of the uterus. By this movement, corresponding to that of the vasa deferentia in man, a certain amount of the mucus normally lining the uterus is forced into the vagina.

This is followed by the rhythmical contraction of the sphincter cunni (analogous to the bulbo-cavernosus), also of the ischio-cavernosus, and deep transversus perinei. The uterus is erected by the powerful contraction of its muscular fibres and round ligaments, while at the same time it descends towards the vagina, its cavity is more and more diminished, and its mucous contents are forced out. When the uterus relaxes after the stage of excitement, it aspirates into its cavity the seminal fluid injected into the vestibule (*Aristotle*, *Bischoff*).

But the suction of the greatly excited uterus is not necessary for the reception of the semen (*Aristotle*). The spermatozoa may wriggle by their own movements from the vagina into the orifice of the uterus (*Kristeller*). The cases of pregnancy where from some pathological causes (partial closure of the vagina or vulva) the penis has not passed into the vagina during coition, prove that the spermatozoa can traverse the whole length of the vagina, and pass into the uterus.

438. FERTILISATION OF THE OVUM.—The **ovum** is fertilised by one **spermatozoon** passing into it.

Swammerdam († 1685) proved that contact of the semen with the ovum was necessary for fertilisation. Spallanzani (1768) proved that the fertilising agent was the spermatozoa, and not the clear filtered fluid part of the semen, and that the spermatozoa, even after being enormously diluted, were still capable of action. Martin Barry (1850) was the first to observe the entrance of a spermatozoon into the ovum of the rabbit. This occurs pretty rapidly, by a boring movement through the vitelline membrane (*Leuckart*). The entrance is effected either through the porous canals or the micropyle (*Keber*, p. 1036).

The sticky surface of the ovum enables the spermatozoon to adhere to it. At the place where the head of the spermatozoon touches the yelk, there is formed opposite to it an elevation of the yelk. As soon as a spermatozoon has penetrated into the yelk, the other spermatozoa are prevented from entering the ovum, owing to the formation of a membrane on the surface of the yelk (*Selenka*). Thermal and chemical stimuli, and mechanical vibrations of unfertilised ova cause ova to lose their power of preventing more than one spermatozoa from entering an ovum (*Hertwig*).

Place of Fertilisation.—The place where fertilisation occurs is either the *ovary*, as indicated by the occurrence of abdominal pregnancy, or the *Fallopian tube*, and the numerous recesses in the latter afford a good temporary nidus for the spermatozoa. This view is supported by the occurrence of tubal pregnancy. Thus, the spermatozoa must be able to pass through the Fallopian tube to the ovary, which is probably brought about chiefly by the movements proper to the spermatozoa themselves. It is uncertain whether the peristaltic movements of the uterus and Fallopian tube are concerned in this process; certainly ciliary movement is not concerned, as the cilia of the Fallopian tube act from above downwards. When once the ovum has passed unfertilised into the uterus, it is not fertilised in the uterus. It is assumed that the ovum reaches the uterus within 2 to 3 weeks (in the bitch, 8 to 14 days).

Twins occur in 1 in 87 pregnancies, but oftener in warm climates; triplets, 1 : 7600; four at a birth, 1 : 330,000. More than six at a time have not been observed. The average number of pregnancies in a woman is $4\frac{1}{2}$.

Superfecundation.—By this term is understood the fertilisation of two ova at the *same menstruation*, by two different acts of coition. Thus, a mare may throw a foal and a mule, after being covered first by a stallion and then by an ass. A white and black child have been born as twins by a woman.

Superfœtation is when a second impregnation takes place at a *later* period of pregnancy, as in the second or third month. This, however, is only possible in a double uterus, or when menstruation persists until the time of the second impregnation. It is said to occur frequently in the hare.

Hybrids are produced when there is a cross between *different species* (horse, ass, zebra—dog, jackal, wolf—goat, ibex—goat, sheep—species of llama—camel, dromedary—tiger, lion—species of pheasant—goose, swan—carp, crucian—species of butterflies). Most hybrids are sterile, especially as regards the formation of properly formed spermatozoa; while the hybrid females are for the most part fertile with the male of both parents, *e.g.*, the mule; but the characters of the offspring tend to return to those of the species of the parents. Very few hybrids are fertile when crossed by hybrids. In many species of frogs the absence of hybrids is accounted for by the mechanical obstacles to fertilisation of the ova.

Tubal Migration of the Ovum.—Under exceptional circumstances, the ovum discharged from a ruptured Graafian follicle passes into the Fallopian tube of the *other* side, as is proved by the occurrence of tubal pregnancy and pregnancy of an abnormal rudimentary horn of the uterus, in which case the true corpus luteum is found on the *other side* of the ovary. This is spoken of as "**external migration**" (*Kussmaul, Leopold*). This observation coincides with experiment, as granular fluids, *e.g.*, China-ink, when injected into the peritoneal cavity, pass into both Fallopian tubes, and are carried by the ciliated epithelium to the uterus (*Pinner*). In animals, with a double uterus with two orifices, the ova may migrate through the os of the one into the other uterus, a condition which is spoken of as "**internal migration.**"

439. IMPREGNATION—CLEAVAGE—LAYERS OF THE EMBRYO.—

Maturation of the Ovum.—In birds and mammals, important changes occur in the

ovum **before impregnation.** The germinal vesicle comes to the surface and disappears from view, while the germinal spot also disappears. In place of the germinal vesicle, a spindle-shaped body appears. The granular elements of the protoplasmic vitellus arrange themselves around each of the two poles of the spindle, in the form of a star, the double-star, or diaster of Fol—**nuclear spindle** (figs. 796, 797). When this takes place, the *peripheral pole* of the nucleus or altered germinal vesicle, along with some of the cellular substance of the ovum, protrudes upon the surface of the vitellus, where they are nipped off from the ovum in the form of small corpuscles just like an excretory product (fig. 798). These bodies, which are not made use of in the further development and growth of the ovum, are called

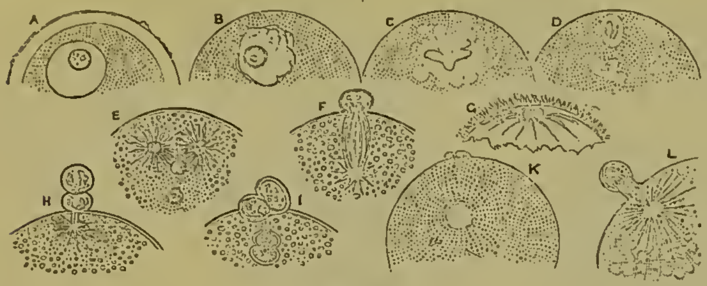


Fig. 796.

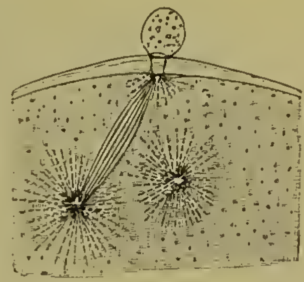


Fig. 797.

Fig. 796.—Formation of polar globules in a star-fish (Asterias glacialis). A, ripe ovum with excentric germinal vesicle and spot; B–E, gradual metamorphosis of germinal vesicle and spot, as seen in the *living egg*, into two asters; F, formation of first polar globule, and withdrawal of the remaining part of the nuclear spindle within the ovum; G, surface view of living ovum with view of first polar globule; H, formation of second polar globule; I, a later stage, showing the remaining internal part of the spindle in the form of two clear vesicles; K, ovum with two polar globules and radial striæ around the female pronucleus; L, extrusion of polar globule. (*Geddes:* A–K, after *Fol;* L, after *O. Hertwig.*) Fig. 797.—Egg of Scorpaena scrofa. The germinal vesicle is extruding a polar globule, and withdrawing towards the centre of the ovum. Near it is the male pronucleus.

polar or **directing globules** (*Fol, Bütschli, O. Hertwig*), although the elimination of small bodies from the yelk was known to Dumortier [1837], Bischoff, P. J. van Beneden, Fritz Müller [1848], Rathke, and others. The remaining part of the germinal vesicle stays within the vitellus and travels back towards the centre of the ovum, to form the **female pronucleus** (*O. Hertwig, Fol, Selenka, E. van Beneden*). [Before, however, the altered germinal vesicle travels downwards again into the substance of the ovum, it divides again as before, and from it is given off the second polar globule, and then the remainder of the germinal vesicle forms the female pronucleus (fig. 796). At the same time the vitellus shrinks somewhat within the vitelline membrane.]

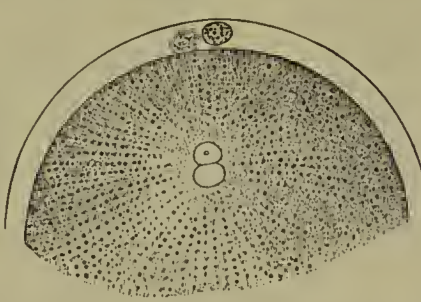


Fig. 798.

Egg of a Star-fish (Asteracanthion) with two extruded polar globules. Male and female pronuclei near each other.

Impregnation.—As a rule, only one spermatozoon penetrates the ovum, and as it does so, it moves towards the female pronucleus, while its head becomes surrounded with a star; it then loses its head and cilium, or tail, the latter only serving as a motor organ, while the remaining middle pieces wells up to form a second new nucleus, the **male pronucleus** (*Fol, Selenka*), or **sperm nucleus** (*Hertwig*). According to Flemming, it is the anterior part of the head, and according to Rein and Eberth, it is the head which is so changed. Thereafter, the male and female pronucleus unite, undergoing amœboid movements at the same time, to form the

new nucleus of the *fertilised ovum.* The female pronucleus receives the male pronucleus in a little depression on its surface. Thereafter the yelk assumes a radiate appearance (*Rein*). [The union of the representatives of the male and female elements forms the *first embryonic segmentation sphere* or **blastosphere**, which divides into two cells, and these again into four, and so on (fig. 799).]

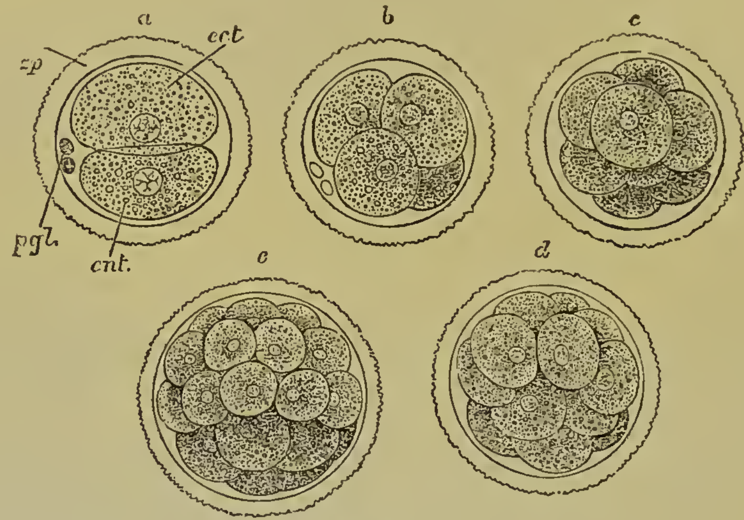


Fig. 799.

Segmentation of a rabbit's ovum. *a*, two-celled stage; *b*, four-celled stage; *c*, eight-celled stage; *de*, many blastomeres showing the more rapid division of the outer-layer cells, and the gradual enclosure of the inner-layer cells; *ect*, outer-layer cells; *ent*, inner-layer cells; *pgl*, polar globules; *zp*, zona pellucida.

In Echinoderms, O. Hertwig and Fol observed that several embryos were formed when, under abnormal conditions, several spermatozoa penetrated an ovum. The male pronuclei, formed from the several spermatozoa, then fused each with a fragment of the female pronucleus. Under similar circumstances, Born observed in amphibians abnormal cleavage, but no further development.

Cleavage of the Yelk.—In an ovum so fertilised the yelk contracts somewhat around the newly-formed nucleus, so that it becomes slightly separated from the vitelline membrane, and for the first time the nucleus and the yelk divides into two nucleated spheres. This process is spoken of as a **complete cleavage** or **fission** (fig. 799). Each of these two cells again divides into two, and the process is repeated, so that 4, 8, 16, 32, and so on, spheres are formed (fig. 800). This constitutes the cleavage of the yelk, and the process goes on until the whole yelk is subdivided into numerous small, nucleated spheres, the "**mulberry mass**" or "**segmentation spheres**" or "**morula,**" or the protoplasmic primordial spheres (20 to 25 μ) which are devoid of an envelope. [Each cell divides by a process of mitosis. According to Van Beneden, the segmentation begins in 1–2 hours after the union of the pronuclei, and the process is complete in about 75 hours. These primitive cells, from which all the tissues of the future embryo are formed, are called **blastomeres.**]

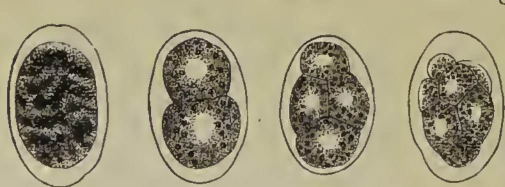


Fig. 800.

Cleavage of the yelk of the egg of Anchylostomum duodenale.

Variation of Lines of Cleavage.—According to the observations of Pflüger, the ova of the frog can be made to undergo cleavage in very different directions, according to the angle between the axis of the egg and the line of gravitation. This of course we can alter as we

please, by placing the eggs at any angle to the line of gravitation. By the axis of the ovum is meant a line connecting the centre of the black surface and the middle of the white part, which, in the fertilised ovum, is always vertical. In such cases of abnormal cleavage the deposition of the organs takes place from other constituents of the egg than those from which they are formed under normal conditions. Under normal circumstances, according to Roux, the first line of cleavage in the frog is in the same direction as the central nervous system. The second intersects the first at a right angle, so as to divide the mass of ovum into two *unequal* parts, the larger of which forms the anterior part of the embryo.

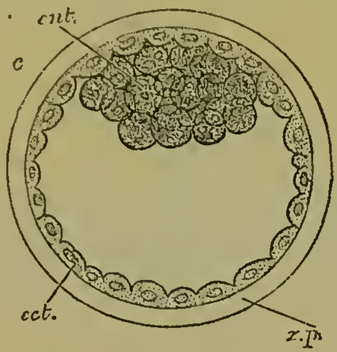


Fig. 801.

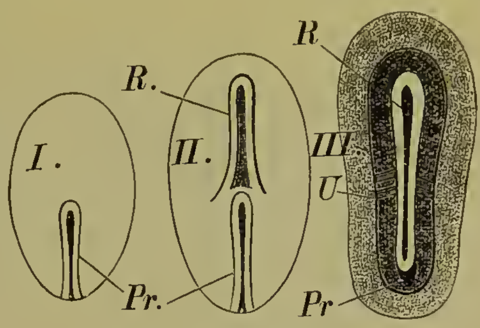


Fig. 802.

Fig. 801.—Blastodermic vesicle of a rabbit. *ect*, ectoderm, or outer layer of cells; *ent*, inner layer of cells. Fig. 802.—*Pr*, primitive streak; *R*, medullary groove; *U*, first protovertebra.

Blastoderm.—During this time the ovum is enlarging by absorption of fluid into its interior. All the cells, from mutual pressure against each other, become polyhedral, and are so arranged as to form a cellular envelope or bladder, the **blastoderm** or **germinal membrane**, which lies on the internal surface of the vitelline membrane (*De Graaf*, *v. Baer*, *Bischoff*, *Coste*). A small part of the cells not used in the formation of the blastoderm is found on some part of the latter. [In the ovum of the **bird**, where there is only **partial segmentation**, the blastoderm is a small round body resting on the surface of the yolk, under the vitelline membrane, so that it does not completely surround the yolk, or a hollow cavity, as in mammals. In mammals, this cavity is called the **segmentation cavity**.] The hollow sphere, composed of cells, is called the **blastodermic vesicle** or **blastula** (*Hæckel*, *Reichert*) (fig. 803), and in the human embryo it is formed at the 10th to 12th day, in the rabbit at the 4th, the guinea-pig at the 3½, the cat 7th, dog 11th, fox 14th, ruminantia at the 10th to 12th day, and the deer at the 60th day.

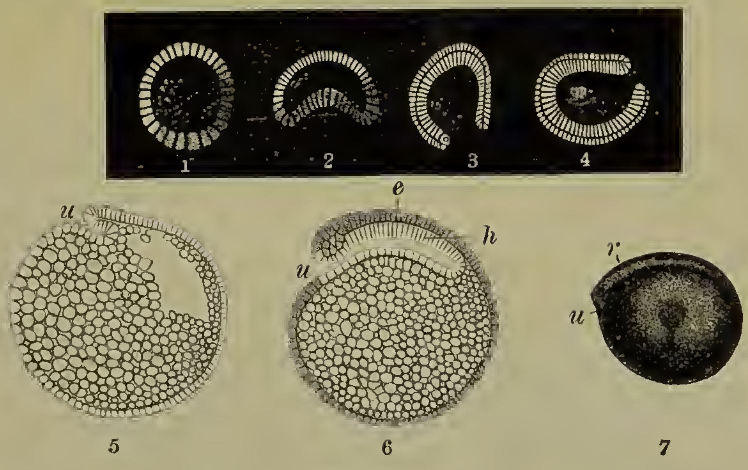


Fig. 803.

1–4, Formation of the hypoblast by invagination of the blastula and the gastrula (4) thereby produced in Amphioxus. 5, The beginning, and 6, the continuation of the formation of the hypoblast by invagination in Petromyzon. *u*, blastopore; *e*, epiblast; *h*, hypoblast in vertical section. 7, The ovum at this stage seen from the side; *r*, neural groove.

The blastula of amphioxus is represented diagrammatically in fig. 803, 1, as a

single layer of cells enclosing a spherical cavity. The blastula undergoes changes whereby two cellular layers are formed, by the invagination of a part of the surface (fig. 803, 2,) which goes on until it touches the inner surface of the part of the layer lying opposite to it (fig. 803, 3, 4). In this stage it is called **gastrula** (*Hæckel*), the outer layer is the **ectoderm** or **epiblast**, the inner the **endoderm** or **hypoblast**, the opening is the **blastopore**, and the cavity the primitive intestine. In vertebrates the blastopore closes completely.

The formation of the hypoblast (fig. 803, 6, *h*) is shown clearly by the invagination in the region of the blastopore in the ovum of the lamprey or petromyzon, and shown diagrammatically in fig. 803, 5, 6, 7, where one can see how, from the blastopore (*u*) invagination takes place until the epiblast (*e*), and hypoblast (*h*), are arranged the one over the other, and below the hypoblast is the primitive intestinal cavity.

It is assumed that the first stages in the embryo exhibit similar appearances and transformation in the vertebrata. According to Van Beneden, the ovum after complete segmentation consists of two layers, the epiblast (fig. 804, I, *e*), which lies next the zona pellucida, *z*, and the hypoblast (*h*). The blastopore or primitive mouth leads to the cavity of the ovum. When the blastoderm grows to 2 mm. (rabbit), whereby the vitelline membrane is distended to a very thin delicate membrane, then at one part of it there appears the **germinal area**, the area

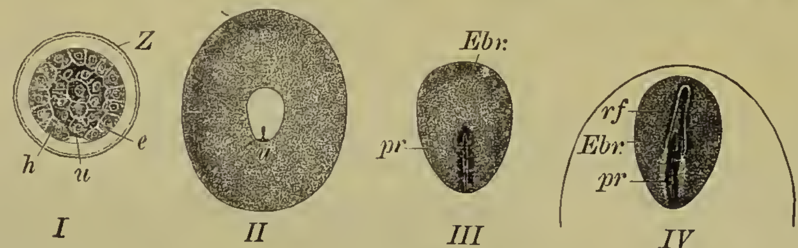


Fig. 804.

I. Ovum of rabbit. *Z*, zona pellucida ; *e*, epiblast ; *h*, hypoblast ; *u*, blastopore. II. Ovum of rabbit with the clear embryonal area ; at *u* is the first formation of the primitive streak. III. *Ebr*, Position of the embryo at a slightly older stage ; *pr*, primitive streak. IV. more advanced still (7th day). Above the primitive streak (*pr*) is the first indication of the neural groove.

germinativa, or the embryonal shield (*Coste*, *Kölliker*). Minute investigation discovers at its margin a small elongated spot (*u*), from which the duplication of the blastoderm proceeds, and which is regarded as the blastopore. From the blastopore the hypoblast continues to grow in the area of the embryonal area, so that the blastoderm ultimately forms a completely closed sac with double walls. The position of the blastopore (II, *u*) becomes later the primitive streak (III. *pr*).

The primitive streak, like the blastopore in vertebrata, is a temporary structure.

The embryonal area soon becomes more pear-shaped, and afterwards biscuit-shaped. The parts of the embryonal area adjoining the blastoderm become more transparent, so that there is a clear area—**area pellucida**—in the centre, which is surrounded by a darker area—**area opaca**. At the same time the surface of the zona pellucida develops numerous small, hollow, structureless villi, and is called the **primitive chorion** (fig. 811, I and vii.).

In mesoblastic ova, *e.g.*, birds, there is only partial cleavage of the yelk. The cells so produced unite to form the **blastoderm**, which consists of two layers, the epiblast and hypoblast. In the blastoderm of the fowl a structure corresponding to the blastopore has been discovered (fig. 805, A, *u*). At first it is short, but it gradually elongates, and is continued or becomes the primitive streak (B,C). In birds also the hypoblast seems to be formed by invagination, and is shown in fig. 805,

E, which represents a sagittal section of a blastoderm. From the blastopore (*u*), the hypoblast (*h*) is pushed under the epiblast, and both membranes rest on the cavity of the primitive intestinal canal (*c*), which is filled with fluid.

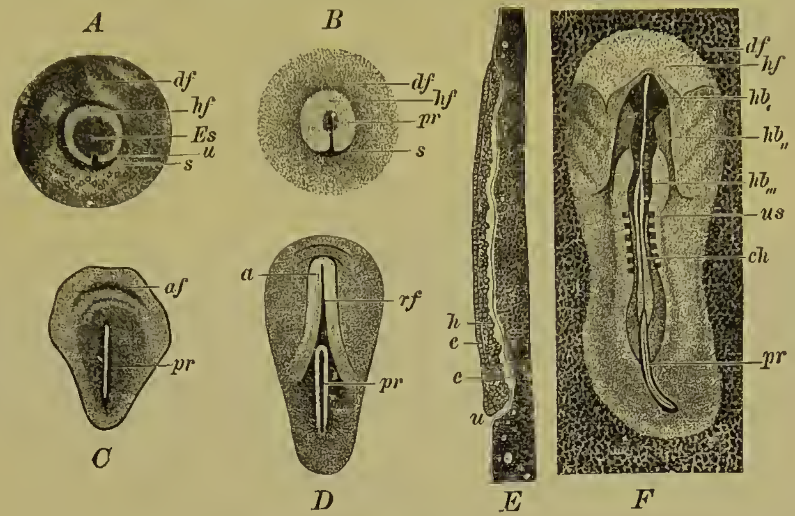


Fig. 805.

A, Blastoderm of a hen's egg at the first hour of incubation. *df*, area opaca ; *hf*, area pellucida ; *Es*, position of embryo ; *u*, position from which the hypoblast becomes invaginated, or where the blastopore has a sickle-shaped form (*s*). *B*, preparation slightly more advanced ; *pr*, primitive streak. *E*, Longitudinal section of a blastoderm at this stage ; *u*, blastopore ; *e*, epiblast ; *h*, hypoblast, and below the latter the primitive intestine *c*. *C*, *pr*, primitive streak, and the first appearance of the amnion, *af*. *D*, embryonal shield with the neural groove, *rf*, formed in front of the primitive streak, *pr* (18 hours). *F*, hen's blastoderm at 33 hours ; *pr*, primitive streak gradually disappearing ; *df*, opaque, and *hf*, clear area ; $hb_{,}$, $hb_{,,}$,$hb_{,,,}$ the primary cerebral vessels ; *us*, protovertebræ ; *ch*, chorda dorsalis.

At the posterior part, or narrow end of the embryonic shield, the **primitive streak** (fig. 802, I, *Pr*) appears at first as an elongated opaque circular thickening, and later as a longer streak or groove, the **primitive groove.** [The opacity is due to the fact that there are several layers of cells in this region (fig. 806). In a transverse section through the primitive streak, three layers of cells are seen. They

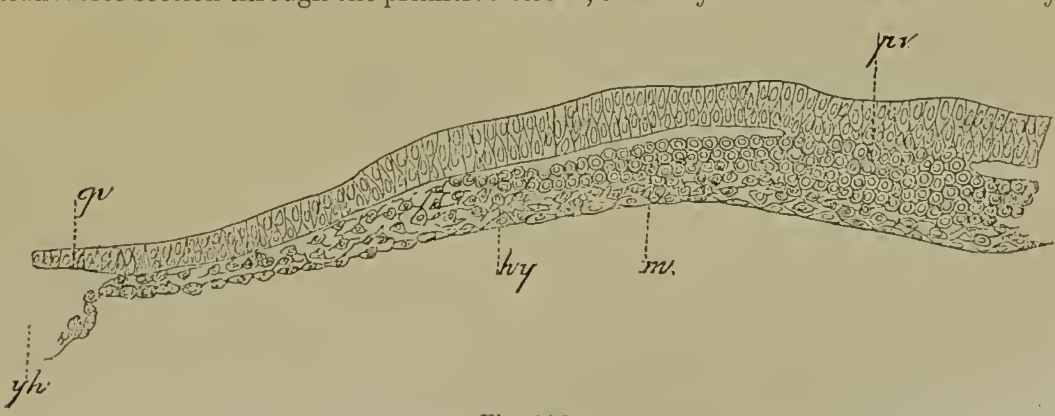


Fig. 806.

Transverse section of the primitive streak of a fowl's blastoderm. *ep*, epiblast ; *hy*, hypoblast ; *m*, mesoblast ; *pv*, primitive groove ; *yh*, yelk of germinal wall.

form part of the middle layer or mesoblast, and are originally derived from the hypoblast. These cells fuse with those of the epiblast. The remainder of the hypoblastic cells retain their stellate character.] At the same time a new layer of

cells is developed between the epiblast and hypoblast, the **mesoderm** or **mesoblast** (fig. 806, I), which soon extends over the embryonal area, and into the blastoderm. [There has been much discussion as to the origin of the mesoblast, but in vertebrates it seems to be originally developed from the hypoblast. Fig. 807 shows a portion of the hypoblast in its axial part, in process of forming the notochord, which is described as mesoblastic.] Blood-vessels are formed within the mesoblast, and are distributed over the blastoderm to form the area vasculosa.

Medullary Groove.—A longitudinal groove, the medullary groove, is formed at the anterior part of the embryonal shield, but it gradually extends posteriorly, embracing the anterior part of the primitive streak with its divided posterior end, while the primitive streak itself gradually becomes relatively and absolutely smaller and less distinct, until it disappears altogether (fig. 802, I, and II, *Pr*).

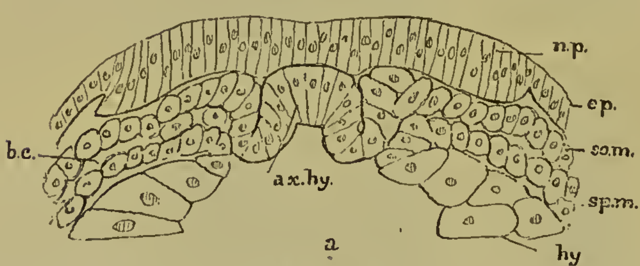


Fig. 807.

Transverse section of an embryo newt. *a*, mesenteron; *ax. hy*, axial hypoblast, forming the notochord; *bc*, cœlom or body-cavity; *ep*, epiblast; *hy*, digestive hypoblast; *so.m*, somatic mesoblast; *sp.m*, splanchnic mesoblast; *n.p*, neural plate.

The position of the embryo is indicated by the central part becoming more transparent,—the **area pellucida**,—which is surrounded by a more opaque part—the **area opaca**. [The area opaca rests directly upon the white yelk in the fowl, and it takes no share in the formation of the embryo, but gives rise to structures which are temporary, and are connected with the nutrition of the embryo. The embryo is formed in the area pellucida alone.]

From the **epiblast** [*neuro-epidermal layer*] are developed the central nervous system and epidermal tissues, including the epithelium of the sense-organs.

From the **mesoblast** are formed most of the organs of the body [including the vascular, muscular, and skeletal systems, and, according to some, the connective - tissue. It also gives rise to the generative glands and excretory organs].

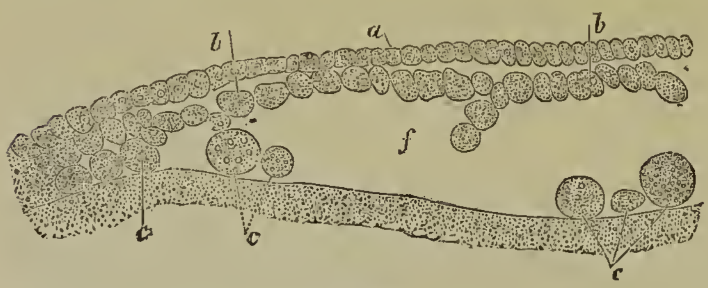


Fig. 808.

Vertical section of part of the unincubated blastoderm of a hen. *a*, epiblast; *b*, hypoblast; *c*, formative cells resting on white yelk; *f*, archenteron.

From the **hypoblast** *epithelio-glandular layer* [which is the secretory layer], arise the intestinal epithelium, and that of the glands which open into the intestine. The notochord is also formed from its axial portion. [The mouth and anus, being formed by an inpushing of the epiblast, are lined by epiblast, and are sometimes called the **stomodæum** and **proctodæum** respectively.]

[**Structure of the Blastoderm** (fig. 808).—Originally it is composed of only two layers, and in a vertical section of it the **epiblast** consists of a single row of nucleated granular cells, arranged side by side, with their long axes placed vertically. The **hypoblast** consists of larger cells than the foregoing, although they vary in size. They are spherical and very granular, so that no nucleus is visible in them. The cells form a kind of network, and occur in more than one layer, especially at

the periphery. It rests on white yolk, and under it are large spherical refractive cells, spoken of as **formative cells** (*c*).]

The cells of the epiblast, and especially those of the hypoblast, nourish themselves by the direct absorption and incorporation of the constituents of the yolk into themselves. The amœboid movements of these cells play a part in the process of absorption. The absorbed particles are changed, or, as it were, digested within the cells, and the product used in the processes of growth and development (*Kollmann*).

[**Division of cells.**—Although a **cell** is defined as a "nucleated mass of living protoplasm," recent researches have shown that, from a histological as well as from a chemical point of view, a cell is really a very complex structure. The apparently homogeneous cell-substance is traversed by a fine **plexus of fibrils**, with a homogeneous substance in its meshes, while a similar network of fibrils exists within the nucleus itself (fig. 809).]

[The **nucleus** of a typical resting cell is a spherical vesicle, consisting of the following parts:—

(1) An outer investing **nuclear membrane**.
(2) A **plexus of fibrils** in its substance or chromatin network.
(3) **Nucleoli**.
(4) A semi-liquid substance in the meshes of the network.

The plexus of fibrils has also been called—"the **nuclear network** of fibrils" "**chromatin**," "**nucleoplasm**," "**karyoplasma**," and "**karyomiton**." The network stains readily with pigments, hence the name "**chromatin**" given to it by Flemming. It seems to be identical with nuclein, and the nodal points of the network give a dotted or granular appearance to the nucleus, especially when it is examined with a low power. In the meshes of the network lie **nucleoli**, which seem to differ in constitution, and perhaps in function. According to Flemming, there are principal and accessory nucleoli in some nuclei. In Carnoy's nomenclature the several parts are spoken of as a fine *reticulum* of fibrils, enclosing in its meshes a fluid—the *enchylema*—which contains various particles in suspension. Under the term "chromatin" is included the network and the nucleoli. The nuclear fluid or matrix or substance lying in the meshes of the nucleus has been called "interfibrillar substance" and **achromatin**, because it does not stain readily with dyes. Part of the achromatin forms the "nuclear spindle" in the process of mitosis. It is to be noted that the names "chromatin" and "achromatin" depend on the histological and not on the chemical characters of these structures.]

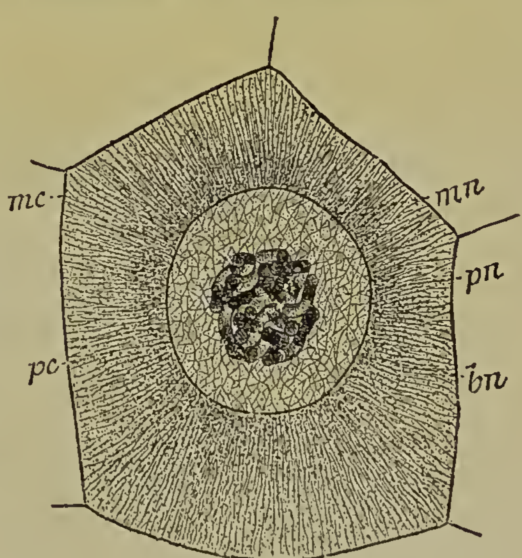


Fig. 809.

Fig. 809.—Typical nucleated cell of the intestinal epithelium of a flesh-maggot. *mc*, membrane of cell; *mn*, membrane of nucleus; *pc*, cellular protoplasm, with the radiating *reticulum*, and the *enchylema* enclosed in its meshes; *pn*, plasma of nucleus; *bn*, nuclear filament showing numerous twists.

[**Direct Cell-division.**—A cell may **divide directly**, as it were, by simple cleavage, and in the process the nucleus usually divides before the cell protoplasm. This is the process of **amitosis**. The nucleus becomes constricted in the centre, has an hour-glass shape, and soon divides into two.]

[**Indirect Cell-Division.**—Recent observations, confirmed by a great number of investigators, conclusively prove that the process of division in cells is a very complicated one, the changes in the nucleus being very remarkable. The terms **karyokinesis, mitosis,** or **indirect division** have been applied to this process. Fig. 810 shows the successive changes that take place in the nucleus. Suppose a nucleus to be in the **resting** stage; when division is about to take place, the chromatin or **intranuclear network** (A, B) passes into a **convolution** of fibrils, while the nuclear envelope becomes less distinct, the fibrils at the same time becoming thicker and forming loops, which gradually arrange themselves around a centre (C and D) in the form of a **wreath, rosette,** or **spirem** (C). Each loop then splits longitudinally, and at the same time the **achromatic spindle** or **nuclear spindle** appears, so that the nucleus exhibits two poles corresponding to the poles of the spindle. The chromatin threads pass towards the centre of the nucleus where they are grouped at its equator and form the equatorial stage or **monaster** (D). The threads or loops produced by division of the original loops now tend to pass towards the two poles of the nucleus, *i.e.*, towards the two poles of the nuclear spindle, forming the **pithode** or **barrel** stage (E). This stage has been called by Waldeyer **metakinesis.**

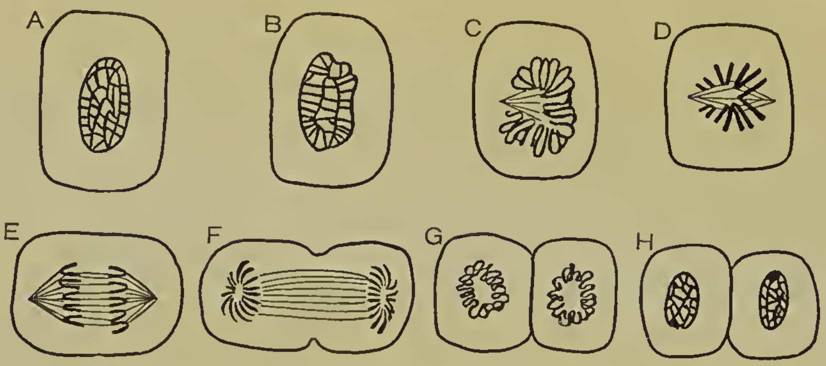


Fig. 810.

Mitosis. A, nuclear reticulum, resting state; B, preparing for division; C, wreath stage, with appearance of nuclear spindle; D, monaster stage; E, barrel stage with the nuclear spindle; F, disaster stage; G daughter wreath stage; H, daughter cells, passing to resting stage.

The two groups of loops then separate still further, and arrange themselves so as to form a **diaster,** or double star or **daughter stars,** the two groups being separated by a substance called the **equatorial plate.** Each of the groups of fibrils becomes more elongated, and forms a nuclear spindle, which indicates the position of a new nucleus. The protoplasm separates into two parts. In each of these parts the chromatin rearranges itself into an irregular coil, and the whole is called **dispirem** (G), and when division is complete, the chromatin filaments assume the form seen in a resting nucleus. This whole complex process may be accomplished in 1 to 4 hours. The separate groups of fibrils again become convoluted, each group gets a nuclear membrane, while the cell protoplasm divides, and two **daughter nuclei** are obtained from the original cell.]

[The following scheme represents some of the more important changes:—

Mother nucleus.	*Daughter nuclei.*
1. Network.	8. Network.
2. Convolution.	7. Convolution.
3. Wreath or Spirem.	6. Dispirem.
4. Aster.	5. Diaster.

Equatorial grouping of chromatin and nuclear spindle.]

440. STRUCTURES FORMED FROM THE EPIBLAST.—Laminæ Dorsales.—The medullary groove upon the epiblast (also called outer, serous, sensorial, corneal, or animal layer) becomes deeper (fig. 811, II). The two longitudinal elevations or **laminæ dorsales** consist of a thickening of the epiblast, and grow up over the medullary groove, thus forming the **neural groove.** Ultimately, however, the laminæ dorsales meet each other and coalesce by their free edges in the middle

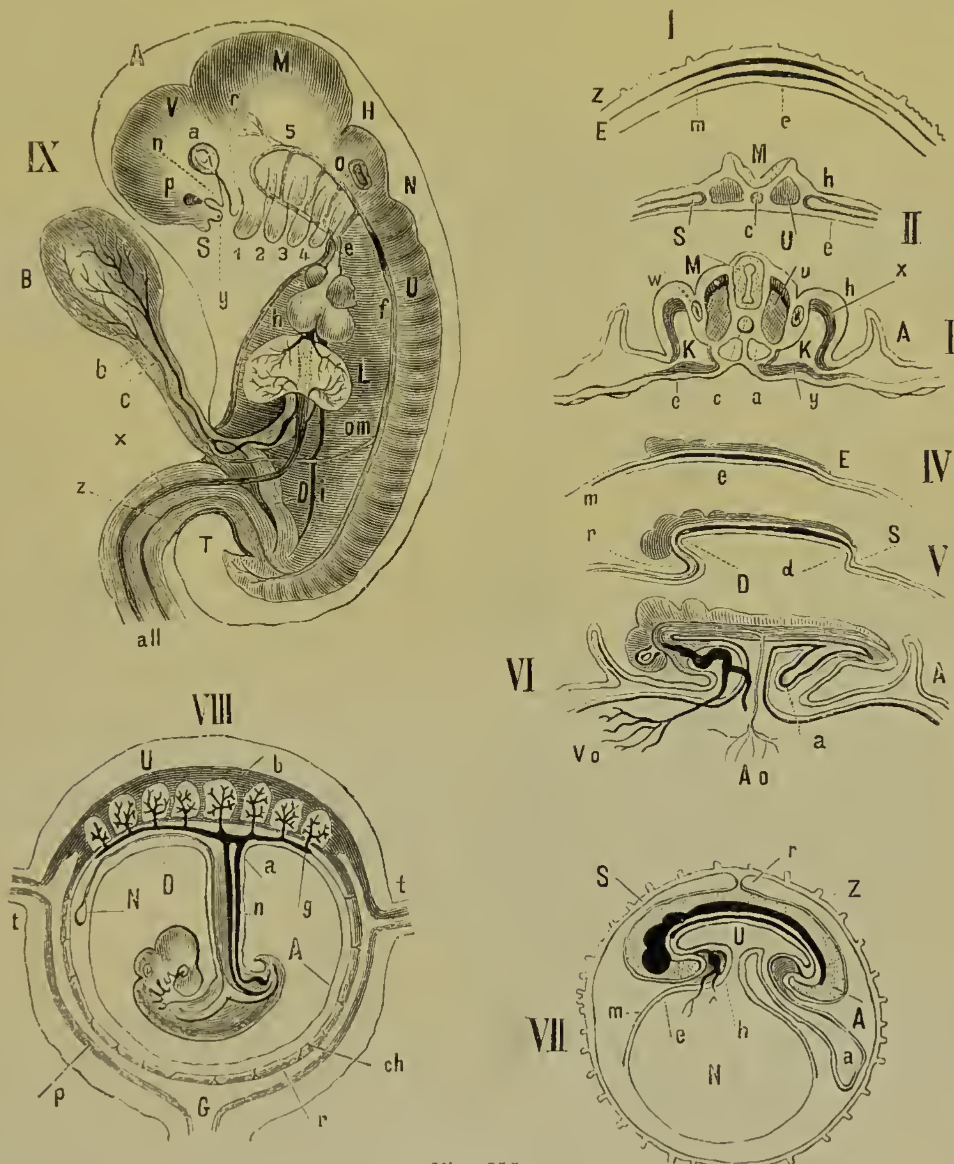


Fig. 811.

I, The three layers of the blastoderm of a mammalian ovum—Z, zona pellucida ; E, epiblast ; *m*, mesoblast ; *e*, hypoblast. II, Section of an embryo, with six protovertebræ at the 1st day—M, medullary groove ; *h*, somatopleure ; U, protovertebra ; *c*, chorda dorsalis ; S, the lateral plates divided into two ; *e*, hypoblast. III, Section of an embryo chick at the 2nd day in the region behind the heart—M, medullary groove ; *h*, outer part of somatopleure ; *u*, protovertebra ; *c*, chorda ; *w*, Wolffian duct ; K, cœlom ; *x*, inner part of somatopleure ; *y*, inner part of splanchnopleure ; A, amniotic fold ; *a*, aorta ; *e*, hypoblast. IV, Scheme of a longitudinal section of an early embryo. V, Scheme of the formation of the head- and tail-folds—*r*, head-fold ; D, anterior extremity of the future intestinal tract ; S, tail-fold, first rudiment of the cavity of the rectum. VI, Scheme of a longitudinal section through an embryo after the formation of the head- and tail-folds—A *o*, omphalo-mesenteric arteries ; V*o*, omphalo-mesenteric veins ; *a*, position of the allantois ; A,

amniotic fold. VII, Scheme of a longitudinal section through a human ovum—Z, zona pellucida; S, serous cavity; r, union of the amniotic folds; A, cavity of the amnion; a, allantois; N, umbilical vesicle; m, mesoblast; h, heart; U, primitive intestine. VIII, Schematic transverse section of the pregnant uterus during the formation of the placenta; U, muscular wall of the uterus; p, uterine mucous membrane, or decidua vera; b, maternal part of the placenta, or decidua serotina; r, decidua reflexa; ch, chorion; A, amnion; n, umbilical cord; a, allantois, with the urachus; N, umbilical vesicle, with D, the omphalo-mesenteric duct; t t, openings of the Fallopian tubes; G, canal of the cervix uteri. IX, Scheme of a human embryo, with the visceral arches still persistent—A, amnion; V, fore-brain; M, mid-brain; H, hind-brain; N, after-brain; U, primitive vertebræ; a, eye; p, nasal pits; S, frontal process; y, internal nasal process; n, external nasal process; r, superior maxillary process of the 1st visceral arch; 1, 2, 3, and 4, the four visceral arches, with the visceral clefts between them; o, auditory vesicle; h, heart, with e, primitive aorta, which divides into five aortic arches; f, descending aorta; om, omphalo-mesenteric artery; b, the omphalo-mesenteric arteries on the umbilical vesicle; c, omphalo-mesenteric vein; L, liver, with venæ advehentes and revehentes; D, intestine; i, inferior cava; T, coccyx; all, allantois, with z, one umbilical artery, and x, an umbilical vein.

line posteriorly. Thus, the open groove is gradually changed into a closed tube—the **medullary** or **neural tube** (fig. 811, III). The cells next the lumen of the tube ultimately become the ciliated epithelium lining the central canal of the spinal cord, while the other cells of the nipped-off portion of the epiblast form the ganglionic part of the central nervous system and its processes.

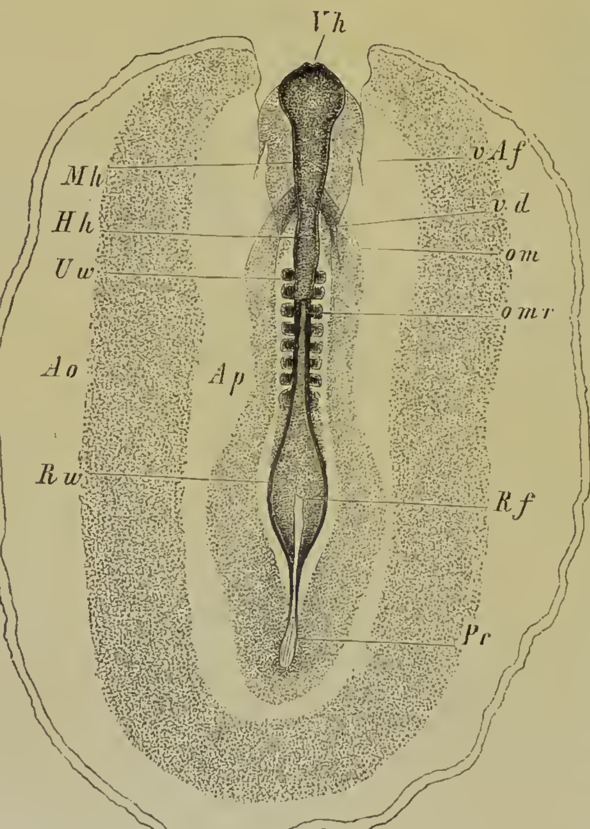


Fig. 812.

Embryo fowl of the 2nd day, ×50. *Ao*, area opaca; *Ap*, area pellucida; *Hh*, hind-brain; *Mh*, mid-brain; *Vh*, fore-brain; *om*, omphalo-mesenteric veins; *omr*, point where the closure of the neural groove is travelling backwards, and to the protovertebræ; *Vw*, muscle-plates; *Rf*, posterior part of widely-open neural groove; *Rw*, neural ridge; *vAf*, anterior amniotic fold.

Primary Cerebral Vesicles.—[The laminæ dorsales unite first in the region of the neck of the embryo, and soon this is followed by the union of those over the future head.] The medullary tube is not of uniform diameter, for at the anterior end it becomes dilated and mapped out by constrictions into the primary vesicles of the brain, which at first are arranged, one behind the other, in the following order, each one being smaller than the one in front of it:—the **fore-brain** (representing the structures from which the cerebral hemispheres are developed); the **mid-brain** (corpora quadrigemina); the **hind-brain** (cerebellum); and the **after-brain** (medulla oblongata); which is gradually continued into the spinal cord (fig. 811, IV and V). The posterior part of the medullary tube has a dilatation at the lumbar enlargement. In birds, the medullary groove remains open in this situation to form a lozenge-shaped dilatation, the sinus rhomboidalis.

While the neural tube is being formed, the primitive streak gradually diminishes, and at last disappears entirely (fig. 805, F).

Cranial Flexures.—The anterior part of the medullary tube curves on itself, especially at the junction of the spinal cord and oblongata, between the mid-brain and hind-brain, and again almost at right angles between the fore-brain and mid-brain. [Thus, a displacement of the primary vesicles is produced, and the head of the future embryo is mapped off.] At first all the cerebral vesicles are devoid of convolutions and sulci. On each side of the fore-brain there grows out a stalked hollow vesicle (fig. 811, VI), the **primary optic vesicle.** The remainder of the epiblast forms the epidermal covering of the body. At an early period we can distinguish the stratum corneum and the Malpighian layer of the skin (§ 283); from the former are developed the hairs, nails, feathers, &c.

Partial Cleavage.—Only a partial cleavage takes place in the eggs of birds and in meroblastic ova, *i.e.*, only the *white yelk* in the neighbourhood of the cicatricula divides into numerous segmentation spheres (*Coste*, 1848). The cells arrange themselves in two layers lying one over the other. The upper layer or *epiblast* is the larger, and contains small pale cells; the lower layer, or *hypoblast*, which at first is not a continuous layer, ultimately forms a continuous layer, but its periphery is smaller than the upper layer, while its cells are larger and more granular.

Between the epiblast and hypoblast there is formed, from the primitive streak as a product of cell proliferation, the **mesoblast**, which is said by Kölliker to be due to the division of the cells of the epiblast. It gradually extends in a peripheral direction between the two other layers. All the three layers grow at their periphery. In the mesoblast blood-vessels are developed. All the three layers, as they grow, come ultimately to enclose the yelk, so that their margins come together at the opposite pole of the yelk.

441. STRUCTURES FORMED FROM THE HYPOBLAST AND MESOBLAST.

—The **hypoblast** forms immediately under the medullary groove, a cylindrical cellular cord, the **chorda dorsalis**, or **notochord**, which is thicker at the tail than

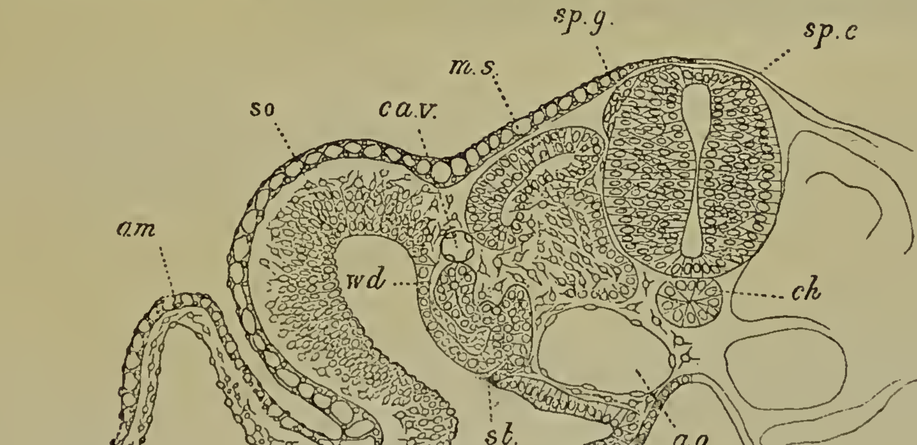


Fig. 813.

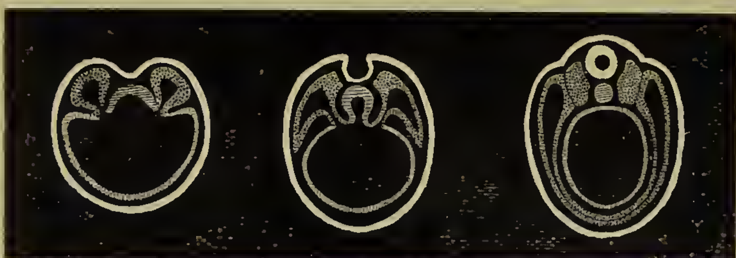
Transverse section of an embryo duck. *am*, amnion; *ao*, aorta; *ca.v*, cardinal vein; *ch*, notochord; *hy*, hypoblast; *ms*, muscle-plate; *so*, somatopleure; *sp*, splanchnopleure; *sp.c*, spinal cord; *sp.g*, spinal ganglion; *st*, segmental tube; *wd*, Wolffian (segmental) duct.

at the cephalic end (fig. 811, II, III, *c*). It is present in all vertebrata, and also in the larval form of the ascidians, but in the latter it disappears in the adult form *Kowalewsky*). In man it is relatively small. It forms the basis of the bodies of

the vertebræ, and around it, as a central core, the substance of the bodies of the vertebræ is deposited, so that they are strung on it, as it were, like beads on a string. After it is formed, it becomes surrounded by a double sheath-like covering (*Gegenbaur*, *Kölliker*).

The **hypoblast** does not undergo any further change at this time; it applies itself to the inner layer of the mesoblast, as a single layer of cells, to form the splanchnopleure.

Protovertebræ.—The cells of the mesoblast, on each side of the chorda, arrange themselves into cubical masses, always disposed in pairs behind each other, the **protovertebræ** (fig. 811, U and *u*, 812, U, *w*). The first pair correspond to the atlas. At a later period each protovertebra shows a marginal cellular area and a nuclear area (fig. 811). Only part of it goes to form a future vertebra. The part of the mesoblast lying external to the protovertebræ, the **lateral plates** (fig. 811, II, *s*), splits into two layers, an upper one and a lower one, which, however, are united by a **median plate** at the protovertebræ. The space between the two layers of the mesoblast is called the **pleuro-peritoneal cavity**, or the **cœlom** of Haeckel (fig. 811, III, K). The upper layer of the lateral plate becomes united to the epiblast, and forms the cutaneo-muscular plate of German authors, or the **somatopleure** (fig. 811, III, *x*; fig. 813, *so*), while the inner one unites with the hypoblast to form the intestinal plate of German authors, or the **splanchnopleure** (fig. 811, III, *y*; fig. 813, *sp*). On the surfaces of these plates, which are directed towards each other, the endothelium lining the pleuro-peritoneal cavity is developed. On the surface of the median plate, directed towards the cœlom, some cylindrical cells, the "**germ epithelium**" of Waldeyer, remain, which form the ovarian tubes and the ova (§ 438).



I. II. III.

Fig. 814.

Scheme of the formation of the chorda and cœlom by invagination from the hypoblast, after Hertwig.

According to Remak, the skin, the muscles of the trunk, and the blood-vessels, and according to His, only the musculature of the trunk, are derived from the somatopleure. Both observers agree that the splanchnopleure furnishes the musculature of the intestinal tract.

Parablastic and Archiblastic Cells. — According to His, the blood-vessels, blood, and connective-tissue are not developed from true mesoblastic cells, but he asserts that for this purpose certain cells wander in from the margins of the blastoderm between the epiblast and hypoblast, these cells being derived from outside the position of the embryo, from the elements of the white yelk. His calls these structures *parablastic*, in opposition to the *archiblastic*, which belong to the three layers of the embryo. Waldeyer also adheres to the parablastic structure of blood and connective-tissue, but he assumes that the material from which the latter is formed is continuous protoplasm, and of equal value with the elements of the blastoderm.

[**Formation of Mesoblast.**—According to Hertwig in the lower vertebrates, the chorda and both walls of the cœlom are derived by protrusion from the hypoblast as is shown schematically in fig. 814. In I is the beginning of the median protrusion (for the chorda) and the two lateral ones (for the walls of the cœlom, but still communicating freely with the hypoblast. In II the part when the protrusion

occurs is narrowed. In III the chorda is separated and appears in transverse section as a round body. In the same way the walls of the cœlom have separated, and show two plates or layers—the somatopleure and splanchnopleure, and between both is the pleuro-peritoneal cavity.

[The following table modified from Quain shows the structures developed from each of the three blastodermic layers (p. 1054):—

From the Epiblast.

The central nervous system (brain and spinal cord): the peripheral and sympathetic nerves.

The epithelium of the organs of special sense.

The epidermis and its appendages, hairs and nails.

The epithelium of all the glands opening on the surface of the skin (mammary, sweat and sebaceous glands).

The muscular fibres of the sweat-glands.

The epithelium of the mouth (except that covering the tongue and the adjacent posterior part of the floor of the mouth, which is derived from the hypoblast) and that of the glands opening into it. The enamel of the teeth.

The epithelium of the nasal passages, of the adjacent upper part of pharynx and of all the cavities and glands opening into the nasal passages.

From the Mesoblast.

The urinary and generative organs (except the epithelium, bladder and urethra).

All the voluntary and involuntary muscles of the body (except the muscular fibres of the sweat-glands.

The whole of the vascular and lymphatic system including the serous membranes and spleen.

The skeleton and all the connective-tissue structures of the body.

From the Hypoblast.

The epithelium of the alimentary canal from the back of the mouth to the anus and that of all the glands which open into this part of the alimentary tube.

The epithelium of the Eustachian tube and tympanum.

The epithelium of the bronchial tubes and air-sacs of the lungs.

The epithelium lining the vesicles of the thyroid body.

The epithelium nests of the thymus.

The epithelium of the urinary bladder and urethra.]

442. FORMATION OF EMBRYO, HEART, PRIMITIVE CIRCULATION. —Head- and Tail-Folds.—Up to this time the embryo lies with its three layers in the plane of the layers themselves. The cephalic end of the future embryo is first raised above the level of this plane (fig. 811, V). In front of, and under the head, there is an inflection or tucking-in of the layers, which is spoken of as the **head-fold** (V, *r*). [It gradually travels backwards, so that the embryo is raised above the level of its surroundings.] The raised cephalic end is hollow, and it communicates with the space in the interior of the umbilical vesicle. The cavity in the head is spoken of as the **head-gut** or **fore-gut** (fig. 811, V, D). The formation of the fore-gut, by the elevation of the head from the plane of the three layers, occurs on the second day in the chick, and in the dog on the 22nd day. The **tail-fold** is formed in precisely the same way, in the chick on the third day, and in the dog on the 22nd day. The tail-fold, S, also is hollow, and the space within it is the **hind-gut**, *d*. Thus, the body of the embryo is supported or rests on a hollow stalk, which at first is wide, and communicates with the cavity of the umbilical vesicle. This duct or communication is called the **omphalo-mesenteric duct**, or the **vitello-intestinal** or **vitelline duct**. The saccular vesicle attached to it in mammals is called the **umbilical vesicle** (fig. 811, VII, N), while the analogous much larger sac in birds, which contains the yellow nutritive yelk, is called the **yelk-sac**. The omphalo-mesenteric or vitelline duct in course of time becomes narrower, and is ultimately obliterated in the chick on the fifth day. The point where it is continuous with the abdominal wall is the abdominal umbilicus, and where it is inserted into the primitive intestine, the intestinal umbilicus.

[Sometimes part of the vitelline duct remains attached to the intestine, and may prove dangerous by becoming so displaced as to constrict a loop of intestine, and thus cause strangulation of the gut.]

Heart.—Before this process of constriction is complete, some cells are mapped off from that part of the splanchnopleure which lies immediately under the head-gut; this indicates the *position of the heart*, which appears in the chick at the end of the first day, as a small, bright red, rhythmically contracting point, the *punctum saliens*, or the στίγμη κινουμένη of Aristotle. In mammals it appears much later.

The **heart** (fig. 811, VI) begins first as a mass of cells, some of which in the centre disappear to form a central cavity, so that the whole looks like a pale hollow bud (originally a pair) of the splanchnopleure. The central cavity soon dilates; it grows, and becomes suspended in the cœlom by a duplicature like a mesentery (meso-cardium), while the space which it occupies is spoken of as the *fovea cardica*. The heart now assumes an elongated tubular form, with its aortic portion directed forwards, and its venous end backward; it then undergoes a slight *f*-shaped curve (fig. 826, 1). From the middle of the 2nd day, the heart begins to beat in the chick, at the rate of about 40 beats per minute. [It is very important to note that at first, although the heart beats rhythmically, it does not contain any nerve-cells.]

From the anterior end of the heart, there proceeds from the bulbus aortæ, the aorta which passes forward and divides into two **primitive aortæ**, which then curve and pass backwards under the cerebral vesicles, and run in front of the proto-vertebræ. Opposite the omphalo-mesenteric duct, each primitive aorta in the chick sends off one, in mammals several (dog, 4 to 5), omphalo-mesenteric arteries (fig. 811, VI, A, *o*), which spread out to form a vascular network within the mesoblast of the umbilical vesicle. From this network there arise the omphalo-mesenteric veins, which run backwards on the vitelline duct, and end by two trunks in the venous end of the tubular heart. In the chick, these veins arise from the sinus terminalis of the future vena terminalis of the area vasculosa. Thus, the **first** or **primitive circulation** is a closed system, and functionally it is concerned in carrying nutriment and oxygen to the embryo. In the bird, the latter is supplied through the porous shell, and the former is supplied up to the end of incubation by the yelk. In mammals, both are supplied by the blood-vessels of the uterine mucous membrane to the ovum. In birds, owing to the absorption of the contents of the yelk-sac, the vascular area steadily diminishes, until ultimately, towards the end of the period of incubation, the shrivelled yelk-sac slips into the abdominal cavity. In mammals, the circulation on the umbilical vesicle, *i.e.*, through the omphalo-mesenteric vessels, soon diminishes, while the umbilical vesicle itself shrivels to a small appendix, and the **second circulation** is formed to replace the omphalo-mesenteric system. The first blood-vessels are formed in the chick, in the **area vasculosa**, outside the position of the embryo, at the last quarter of the first day, before any part of the heart is visible. The blood-vessels begin in vaso-formative cells [constituting the "**blood-islands**" of Pander]. At first they are solid, but they soon become hollow (§ 7, A).

A narrow-meshed plexus of *lymphatics* is formed in the area vasculosa of the chick (*His*), and it communicates with the amniotic cavity (*A. Budge*).

443. FORMATION OF THE BODY.—Body-Wall.—(1) The **cœlom**, or **pleuro-peritoneal cavity**, becomes larger and larger, while at the same time the difference between the body-wall and the wall of the intestine becomes more pronounced. The latter becomes more separated from the protovertebræ, as the middle plate begins to be elongated to form a mesentery. The body-wall, or somatopleure, composed of the epiblast and the outer layer of the cleft mesoblast, becomes thickened by the ingrowth into it of the muscular layer from the muscle-plate, and the position of the bones and the spinal nerves from the protovertebræ. These

grow between the epiblast and the outer layer of the mesoblast (*Remak*). [The **somatopleure**, or parietal lamina, from each side grows forward and towards the middle line, where they meet to form the body-wall, while at the same time the **splanchnopleure**, or visceral lamina, on each side also grow and meet in the middle line, and when they do so, they enclose the intestine. Thus, there is one tube within the other, and the space between is the pleuro-peritoneal cavity.]

(2) **Vertebral Column.**—A dorsally placed structure, called the **muscle-plate** (fig. 813, *ms.*), is differentiated from each of the protovertebræ; the remainder of the protovertebra, the protovertebra proper, coalesces with that on the other side, so that both completely surround the chorda, to form the **membrana reuniens inferior**, in the chick on the 3rd, and in the rabbit on the 10th day, while, at the same time, they close over the medullary tube dorsally, in the chick at the 4th day, to form the **membrana reuniens superior** (*Reichert*). Thus, there is a union of the masses of the protovertebræ in *front* of the medullary tube, which encloses the chorda, and represents the basis of the *bodies* of all the vertebræ, whilst the membrana reuniens superior, pushed between the muscle-plates and the epiblast on the one hand and the medullary tube on the other, represents the position of the entire vertebral *laminæ* as well as the intervertebral ligaments between them. The vertebral column at this membranous stage is in the same condition as the vertebral column of the cyclostomata (Petromyzon).

Spina Bifida.—In some rare cases the membrana reuniens superior is not developed, so that the medullary tube is covered only by the epiblast (epidermis), either throughout its entire extent, or at certain parts. This constitutes the condition of **spina bifida**, or, when it occurs in the head, hemicephalia.

Lastly, parts of the somatopleures also grow towards the middle line of the back, and insinuate themselves between the muscle-plate and the epiblast; thus, the dorsal skin is formed (*Remak*).

In the membranous vertebral column, there are formed the several *cartilaginous* vertebræ, the one behind the other, in man at the 6th to 7th week, although at first they do not form closed vertebral arches; the latter are closed in man about the 4th month. Each cartilaginous vertebra, however, is not formed from a pair of protovertebræ, *i.e.*, the 6th cervical vertebra, from the 6th pair of protovertebræ, but there is a new subdivision of the vertebral column, so that the lower half of the preceding protovertebra and the upper half of the succeeding protovertebra unite to form the final vertebra. While the bodies are becoming cartilaginous the chorda becomes smaller, but it still remains larger in the intervertebral discs. The body of the first vertebra or atlas unites with that of the axis to form its odontoid process, and in addition it forms the arcus anterior atlantis and the transverse ligament (*Hasse*). The chorda can be followed upwards through the ligamentum suspensorium dentis as far as the posterior part of the sphenoid bone.

The **histogenetic formation of cartilage** from the indifferent formative cells takes place by division and growth of the cells, until they ultimately form clear nucleated sacs. The cement substance is probably formed by the outer parts of the cells (parietal substance) uniting and secreting the intercellular substance. It is supposed by some that the latter contains fine canals, which connect the protoplasm of the adjoining cells.

Visceral Clefts and Arches.—Each side of the cervical region contains four slit-like openings—the **visceral clefts** or **branchial openings** (*Rathke*); in the chick, the upper three are formed at the third, and the fourth on the 4th day. Above the slits are thickenings of the lateral wall, which constitute the **visceral** or **branchial arches** (fig. 819). The clefts are formed by a perforation from the fore-gut, but this, perhaps, does not always occur in the chick, mammal, and man (*His*), and they are lined by the cells of the hypoblast. On each side in each visceral arch, *i.e.*, above and below each cleft, there runs an aortic arch, five on each side (fig. 811, IX). These aortic arches persist in fishes. In man, all the slits close,

except the uppermost one, from which the auditory meatus, the tympanic cavity, and the Eustachian tube are developed. The four visceral arches are for the most part made use of later for other formations (p. 1072).

Primitive Mouth and Anus.—Immediately under the fore-brain, in the middle line, is a thin spot, where there is at first a small depression, and ultimately a rupture, forming the **primitive oral aperture**, which represents both the mouth and the nose. Similarly, there is a depression at the caudal end, and the depression ultimately deepens, thus communicating with the hind-gut to form the anus. When the latter part of the process is incomplete, there is **atresia ani**, or imperforate anus. Several processes are given off from the primitive intestine, including the hypoblast and its muscular layers, to form the lungs, the liver, the pancreas, the cæcum (in birds), and the allantois.

The **extremities** appear at the sides of the body as short unjointed stumps or projections at the 3rd or 4th week in the human embryo.

444. AMNION AND ALLANTOIS.—**Amnion.**—During the elevation of the embryo from its surroundings, immediately in front of the head (at the end of the 2nd day in the chick), there rises up a fold consisting of the epiblast and the outer layer of the mesoblast, which gradually extends to form a sort of hood over the cephalic end of the embryo (fig. 811, VI, A). In the same way, but somewhat later, a fold rises at the caudal end, and between both along the lateral borders similar elevations occur, the lateral folds (fig. 811, III, A). All these folds grow over the back of the embryo to meet over the middle line posteriorly, where they unite at the 3rd day, in the chick, to form the **amniotic sac.** Thus, a *cavity* which becomes filled with fluid—the **amniotic fluid**—is developed around the embryo [so that the embryo really floats in the fluid of the amniotic sac]. In mammals also the amnion is developed very early, just as in birds (fig. 811, VII, A). From the middle of pregnancy onwards, the amnion is applied directly to the chorion, and united to it by a gelatinous layer of tissue, the tunica media of Bischoff.

Amniotic Fluid.—The amnion, and the allantois as well, are formed only in mammals, birds, and reptiles, which have hence been called **amniota**, while the lower vertebrates, which are devoid of an amnion, are called **anamnia.**

Amniotic fluid. Composition.—The **amniotic fluid** is a clear, serous, alkaline fluid, specific gravity 1007 to 1011, containing, besides epithelium, lanugo hairs, $\frac{1}{2}$ to 2 per cent. of fixed solids. Amongst the latter are albumin ($\frac{1}{10}$ to $\frac{1}{3}$ per cent.), mucin, globulin, a vitellin-like body, some grape-sugar, urea, ammonium carbonate, very probably derived from the decomposition of urea, sometimes lactic acid and kreatinin, calcic sulphate and phosphate, and common salt. About the middle of pregnancy, it amounts to about 1–1·5 kilo. [2·2–3·3 lbs.], and at the end about 0·5 kilo. The amniotic fluid is of fœtal origin, as is shown by its occurrence in birds, and is, perhaps, a transudation through the fœtal membranes. In mammals, the urine of the fœtus forms part of it during the second half of pregnancy (*Gusscrow*). In the pathological condition of **hydramnion**, the blood-vessels of the uterine mucous membrane secrete a watery fluid. The fluid preserves the fœtus, and also the vessels of the fœtal membranes from mechanical injuries; it permits the limbs to move freely, and protects them from growing together; and, lastly, it is important for dilating the os uteri during labour. The amnion is capable of contraction at the 7th day in the chick; and this is due to the smooth muscular fibres which are developed in the cutaneous plate in its mesoblastic portion, but nerves have not been found.

Allantois.—From the anterior surface of the caudal end of the embryo there grows out a small double projection, which becomes hollowed out to form a sac projecting into the cavity of the cœlom or pleuro-peritoneal cavity (fig. 811); it constitutes the **allantois** and is formed in the chick before the 5th day, and in man during the 2nd week. Being a true projection from the hind gut, the allantois has two layers, one from the hypoblast, and the other from the muscular layer, so that it is an offshoot from the splanchnopleure. From both sides, there pass on to the allantois the **umbilical arteries** from the hypogastric arteries, and

they ramify on the surface of the sac. The allantois grows, like a urinary bladder gradually being distended, in front of the hind-gut in the pleuro-peritoneal cavity towards the umbilicus; and lastly, it grows out of the umbilicus, and projects beyond it alongside the omphalo-mesenteric or vitelline duct, its vessels growing with it (fig. 811, VII, *a*); but, after this stage, it behaves differently in birds and mammals.

In **birds**, after the allantois passes out of the umbilicus, it undergoes great development, so that within a short time it lines the whole of the interior of the shell as a highly vascular and saccular membrane. Its arteries are at first branches of the primitive aortæ, but with the development of the posterior extremities they appear as branches of the hypogastric arteries. Two allantoidal, or *umbilical veins*, proceed from the numerous capillaries of the allantois. They pass backward through the umbilicus, and at first unite with the omphalo-mesenteric veins to join the venous end of the heart. In birds this circulation on the allantois, or *second circulation*, is **respiratory** in function, as its vessels serve for the exchange of gases through the porous shell. The circulation gradually assumes the respiratory functions of the umbilical vesicle, as the latter gradually becomes smaller and smaller, and ceases to be a sufficient respiratory organ. Towards the end of the period of incubation the chick may breathe and cry within the shell (*Aristotle*)—a proof that the respiratory function of the allantois is partly taken over by the lungs. The allantois is also the **excretory** organ of the urinary constituents. Into its cavity in mammals the ducts of the *primitive kidneys*, or the *Wolffian ducts*, open, but in birds and reptiles, which possess a cloaca, these open into the posterior wall of the cloaca. The primitive kidneys, or Wolffian bodies, consist of many glomeruli, and empty their secretion through the Wolffian ducts into the allantois (in birds into the cloaca), and the secretion passes through the allantois, per the umbilicus, into the peripheral part of the urinary sac. Remak found ammonium and sodium urate, allantoin, grape-sugar, and salts in the contents of the allantois. From the 8th day onwards, the allantois of the chick is contractile (*Vulpian*), owing to the presence of smooth fibres derived from the splanchnopleure. Lymphatics accompany the branches of the arteries (*A. Budge*).

Allantois in Mammals.—In mammals and man, the relation of the allantois is somewhat different. The first part or its origin forms the **urinary bladder**, and from the vertex of the latter there proceeds through the umbilicus a tube, the **urachus**, which is open at first (fig. 811, VIII, *a*). The blind part of the sac of the allantois outside the abdomen is in some animals filled with a fluid like urine. In man, however, this sac disappears during the 2nd month, so that there remains only the vessels which lie in the muscular part of the allantois. In some animals, however, the allantois grows larger, does not shrivel, but obtains through the urachus from the bladder an alkaline turbid fluid, which contains some albumin, sugar, urea, and allantoin. The relations of the umbilical vessels will be described in connection with the fœtal membranes.

445. FŒTAL MEMBRANES, PLACENTA, FŒTAL CIRCULATION.—Decidua.—When a fecundated ovum reaches the uterus, it becomes surrounded by a special covering, which William Hunter (1775) described as the **membrana decidua**, because it was shed at birth. We distinguish the **decidua vera** (fig. 811, VIII, *p*), which is merely the thickened, very vascular, softened, more spongy, and somewhat altered mucous membrane of the uterus. [Sometimes in a diseased condition, as in dysmenorrhœa, the superficial layer of the uterine mucous membrane is thrown off nearly *en masse* in a triangular form (fig. 815). This serves to show the shape of the decidua, which is that of the uterus.] When the ovum reaches the uterus, it is caught in a crypt or fold of the decidua, and from the latter there grow up elevations around the ovum; but these elevations are thin, and soon meet over the back of the ovum to form the **decidua reflexa** (fig. 811, VIII, *r*). At the 2nd to 3rd month there is still a space in the uterus outside the reflexa; in the 4th month, the whole cavity is filled by the ovum. At one part the ovum lies directly upon the d. vera [and that part is spoken of as the **decidua serotina**], but by far the greatest part of the surface of the ovum is in contact with the reflexa. In the region of the d. serotina the **placenta** is ultimately formed.

Structure of the Decidua Vera.—The d. vera at the 3rd month is 4 to 7 mm. thick, and

at the 4th only 1 to 3 mm., and it no longer has any epithelium ; but it is very vascular, and is possessed of lymphatics around the glands and blood-vessels (*Leopold*), and in its loose substance are large round cells (decidua cells—*Kölliker*), which in the deeper parts become changed into fibre cells—there are also lymphoid cells. The uterine glands, which become greatly developed at the commencement of pregnancy, at the 3rd to the 4th month form non-cellular, wide, bulging tubes, which become indistinct in the later months, and in which the epithelium disappears more and more. The **d. reflexa**, much thinner than the vera from the middle of pregnancy, is devoid of epithelium, and is without vessels and glands. Towards the end of pregnancy the two deciduæ unite with each other.

The ovum, covered at first with small hollow **villi**, is surrounded by the decidua. From the formation of the amnion it follows that, after it is closed, a completely closed sac passes away from the embryo to lie next the **primitive chorion**. This membrane is the "serous covering" of v. Baer (fig 811, VII, *s*), or the **false amnion**. It becomes closely applied to the inner surface of the chorion, and extends even into its villi. The allantois proceeding from the umbilicus comes to lie directly in contact with the fœtal membrane ; its sac disappears about the 2nd month in man, but its vascular layer grows rapidly and lines the whole of the inner surface of the chorion, where it is found on the 18th day (*Coste*). From the 4th week the blood-vessels, along with a covering of connective-tissue, branch and penetrate into the hollow cavities of the villi, and completely fill them. At this time the primitive chorion disappears. Thus we have a stage of general vascularisation of the chorion. In the place of the derivative of the zona pellucida we have the vascular villi of the allantois, which are covered by the epiblastic cells derived from the false amnion. This stage lasts only until the 3rd month, when the chorionic villi disappear all over that part of the surface of the ovum which is in contact with the decidua reflexa. On the other hand, the villi of the chorion, where they lie in direct contact with the decidua serotina, become larger and more branched. Thus, there is distinguished the **chorion laeve** and **c. frondosum**.

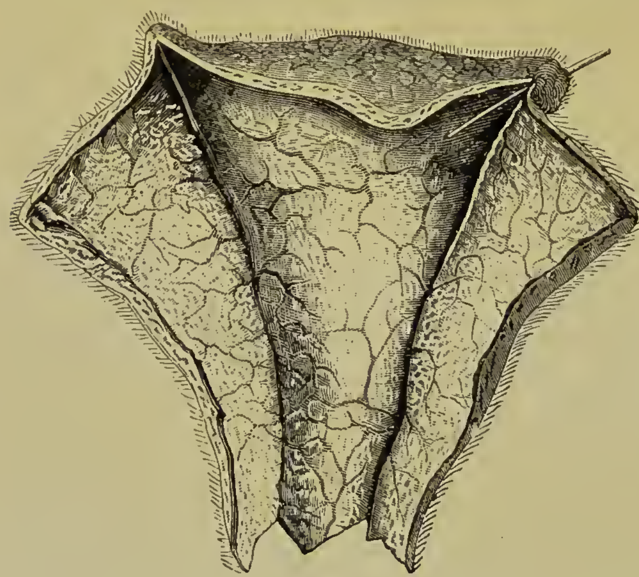


Fig. 815.
A dysmenorrhœal membrane laid open.

The chorion laeve, which consists of a connective-tissue matrix covered externally by several layers of cells, has a few isolated villi at wide intervals. Between the chorion and the amnion is a gelatinous substance (membrana intermedia) or undeveloped connective-tissue.

Placenta.—The large villi of the chorion frondosum penetrate into the tissue of the decidua serotina of the uterine mucous membrane. [It was formerly supposed that the chorionic villi entered the mouths of the uterine glands, but the researches of Ercolani and Turner have shown that, although the uterine glands enlarge during the early months of utero-gestation, the villi do not enter the glands. The villi enter the crypts of the uterine mucous membrane. The glands of the inner layer of the decidua serotina soon disappear.] As the villi grow into the decidua serotina, they push against the walls of the large blood-vessels, which are similar to capillaries in structure, so that the villi come to be bathed by the blood of the mother in the uterine sinuses, or they float in the colossal decidual capillaries (fig.

811, VII, *b*). The villi do not float naked in the maternal blood, but they are covered by a layer of cells derived from the decidua. Some villi, with bulbous ends, unite firmly with the tissue of the uterine part of the placenta to form a firm bond of connection. [The placenta is formed by the mutual intergrowth of the chorionic villi and the decidua serotina.] Thus, it consists of a **fœtal part**, including all the villi, and a **maternal** or **uterine part**, which is the very vascular decidua serotina. At the time of birth both parts are so firmly united that they cannot be separated. Around the margin of the placenta is a large venous vessel, the *marginal sinus* of the placenta. [Friedländer found the uterine sinuses below the placental site blocked by giant cells after the 8th month of pregnancy. Leopold confirms this, and found the same in the serotinal veins.]

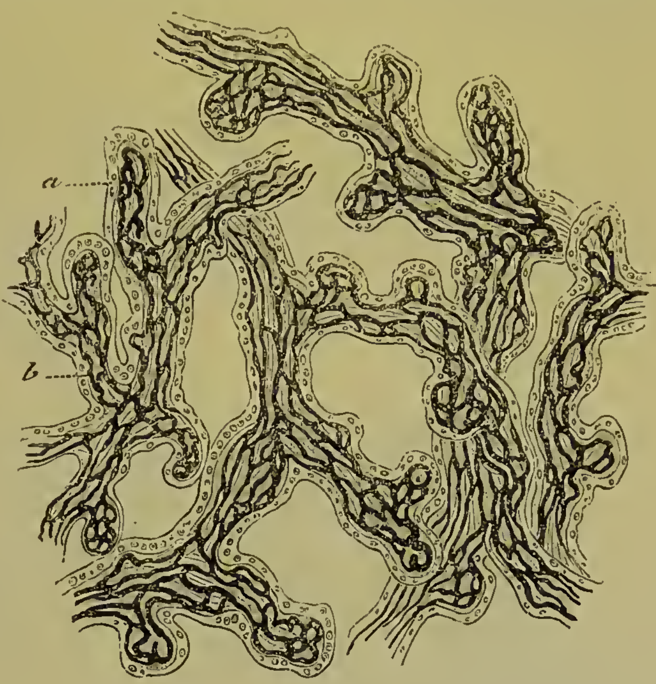


Fig. 816.
Human placental villi. Blood-vessels black.

Functions.—The placenta is the **nutritive, excretory,** and **respiratory** organ of the fœtus (§ 368); the latter receives its necessary pabulum by endosmosis from the maternal sinuses through the coverings and vascular wall of the villi in which the fœtal blood circulates. [The placenta also contains *glycogen.*]

[**Structure.**—A piece of fresh placenta teased in normal saline solution shows the villi provided with lateral offshoots, and consisting of a connective-tissue framework, containing a capillary network with arteries and veins, while the villi themselves are covered by a layer of somewhat cubical epithelium (fig. 816).]

Uterine Milk.—Between the villi of the placenta there is a clear fluid, which contains numerous small, albuminous globules, and this fluid, which is abundant in the cow, is spoken of as the uterine milk. It seems to be formed by the breaking up of the decidual cells. It has been supposed to be nutritive in function. [The maternal placenta, therefore, seems to be a secreting structure, while the fœtal part has an absorbing function. The uterine milk has been analysed by Gamgee, who found that it contained fatty, albuminous, and saline constituents, while sugar and casein were absent.]

The investigations of Walter show that after poisoning pregnant animals with strychnin, morphia, veratrin, curare, and ergotin, these substances are not found in the fœtus, although many other chemical substances pass into it.

[Savory found that strychnin injected into a fœtus in utero caused tetanic convulsions in the mother (bitch), while syphilis may be communicated from the father to the mother through the medium of the fœtus (*Hutchinson*). A. Harvey's record of observations on the crossing of breeds of animals—chiefly of horses and allied species—show that materials can pass from the fœtus to the mother.]

On looking at a placenta, it is seen that its villi are distributed on large areas separated from each other by depressions. This complex arrangement might be compared with the cotyledons of some animals.

The position of the placenta is, as a rule, on the anterior or posterior wall of the uterus, more

rarely on the fundus uteri, or laterally from the opening of the Fallopian tube, or over the internal orifice of the cervix, the last constituting the condition of **placenta praevia**, which is a very dangerous form of placental insertion, as the placenta has to be ruptured before birth can take place, so that the mother often dies from hæmorrhage. The umbilical cord may be inserted in the centre of the placenta (*insertio centralis*), or more towards the margin (*ins. marginalis*), or the cord may be fixed to the chorion laeve. Sometimes, though rarely, there are small subsidiary placentæ (*pl. succenturiata*), in addition to the large one. When the placenta consists of two halves, it is called duplex or bipartite, a condition said by Hyrtl to be constant in the apes of the old world.

Structure of the Umbilical Cord.—The umbilical cord (48 to 60 cm. [20 to 24 inches] long, 11 to 13 mm. thick) is covered by a sheath from the amnion. The blood-vessels make about forty **spiral turns**, and they begin to appear about the 2nd month. [The cause of the twisting is not well understood, but Virchow has shown that capillaries pass from the skin for a short distance on the cord, and they do so unequally, and it may be that this may aid in the production of the torsion.] It contains two strongly muscular and contractile arteries, and one umbilical vein.

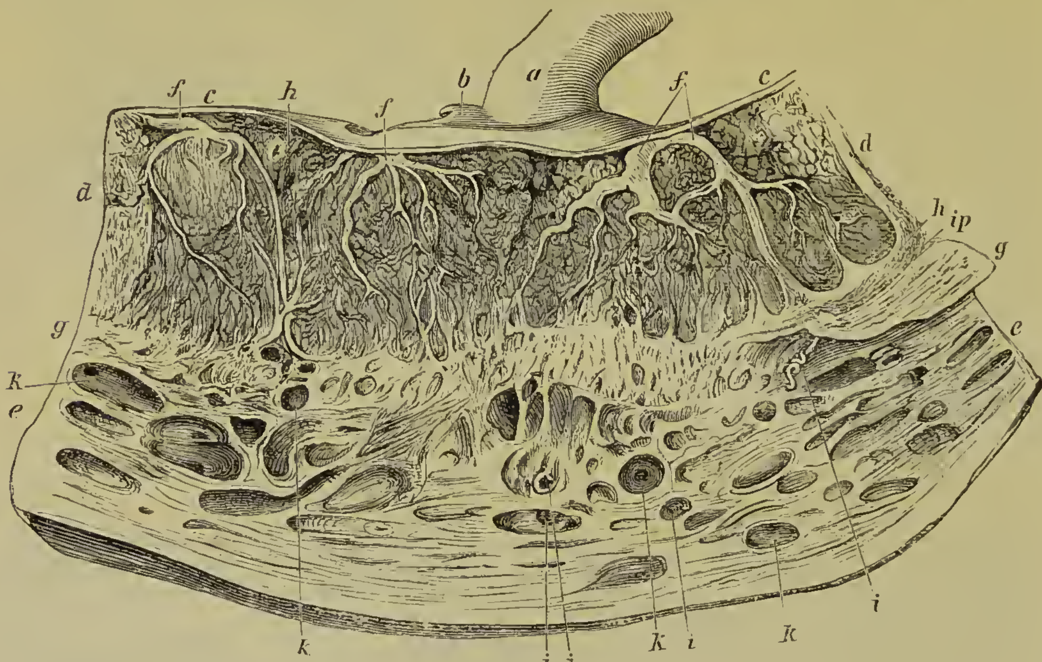


Fig. 817.

Section of the uterine wall with the placenta adhering to it, from a woman 30 weeks pregnant. *a*, root and insertion of the umbilical cord ; *b*, amniotic covering of the placenta and cord ; *c*, chorion ; *dd*, fœtal part of the placenta ; *ee*, uterine wall ; *ff*, complex of placental villi forming the fœtal placenta ; *gg*, decidua ; *hh*, processes of the decidua penetrating into the fœtal placenta ; *ii*, branches of an uterine artery ; *ip*, an artery entering the placenta ; *kkkk*, uterine veins.

The two arteries anastomose in the placenta (*Hyrtl*). In addition, the cord contains the continuation of the urachus, the hypoblastic portion of the allantois (fig. 811, VIII, *a*), which remains until the 2nd month, but afterwards is much shrivelled. The omphalo-mesenteric duct of the umbilical vesicle (N) is reduced to a thread-like stalk (fig. 811, VIII, D). **Wharton's jelly** surrounds the umbilical blood-vessels. Wharton's jelly is a gelatinous-like connective-tissue, consisting of branched corpuscles, lymphoid cells, some connective-tissue fibrils, and even elastic fibres. It yields **mucin**. It is traversed by numerous juice-canals lined by endothelial cells, but other blood- and lymphatic-vessels are absent. Nerves occur 3–8–11 cm. from the umbilicus (*Schott*).

The **foetal circulation**, which is established after the development of the allantois, has the following course (fig. 818):—The blood of the fœtus passes from the hypogastric arteries through the two umbilical arteries, through the umbilical cord to the placenta, where the arteries split up into capillaries. The blood is returned from the placenta by the umbilical vein, although the colour of the blood cannot be distinguished from the venous or impure blood in the umbilical arteries. The umbilical vein (fig. 829, 2, *u*) returns to the umbilicus, passes upwards under the margin of the liver, gives a branch to the vena portæ (*a*), and runs as the **ductus venosus** into the inferior vena cava, which carries the blood into the right auricle. Directed by the Eustachian valve and the tubercle of Lower (fig. 826, 6, *tL*), the great mass of the blood passes through the **foramen ovale** into the left auricle, owing to the presence of the valve of the foramen ovale. From the left auricle it passes into the left ventricle, aorta, and hypogastric arteries, to the umbilical arteries. The blood of the superior vena cava of the fœtus passes from the right auricle into the right ventricle (fig. 826, 6, *Cs*). From the right ventricle it passes into the pulmonary artery (fig. 826, 7, *p*), and through the **ductus arteriosus** of Botalli (*B*) into the aorta. There are, therefore, two streams of blood in the right auricle which cross each other, the descending one from the head through the superior vena cava, passing in front of the transverse one from the inferior vena cava to the foramen ovale.] Only a small amount of the blood passes through the as yet small branches of the pulmonary artery to the lungs (fig. 826, 7, *1*, *2*). The course of the blood makes it evident that the head and upper limbs of the fœtus are nourished by purer blood than the remainder of the trunk, which is supplied with blood mixed with the blood of the superior vena cava. **After birth**, the umbilical arteries are obliterated, and become the lateral ligaments of the bladder, while their lower parts remain as the superior vesical arteries. The umbilical vein is obliterated, and remains as the ligamentum teres, or round ligament of the liver, and so is the ductus venosus Arantii. Lastly, the foramen ovale is closed, and the ductus arteriosus is obliterated, the latter forming the lig. arteriosus.

Fig. 818.
Course of the fœtal circulation.

The **condition of the membranes** where there are more fœtuses than one:—(1) With twins there are two completely separated ova, with two placentæ and two decidual reflexæ. (2) Two completely separated ova may have only one reflexa, whereby the placentæ grow together, while their blood-vessels remain distinct. The chorion is actually double, but cannot be separated into two lamellæ at the point of union. (3) One reflexa, one chorion, one placenta, two umbilical cords, and two amnia. The vessels anastomose in the placenta. In this case there is one ovum with a double yelk, or with two germinal vesicles in one yelk. (4) As in (3), but only one amnion, caused by the formation of two embryos in the same blastoderm of the same germinal vesicle.

Formation of the fœtal membranes.—The oldest mammals have no placenta or umbilical vessels; these are the **Mammalia implacentalia**, including the monotremata and marsupials. The second group includes the **Mammalia placentalia.** Amongst these (a) the **non-deciduata** possess only chorionic villi supplied by the umbilical vessels, which project into the depressions of the uterine mucous membrane, and from which they are pulled out at birth (Pl. diffusa, *e.g.*, pachydermata, cetacea, solidungula, camelidæ). In the *ruminants*, the villi are arranged in groups or **cotyledons**, which grow into the uterine mucous membrane, from which they are pulled out at birth. (b) In the **deciduata**, there is such a firm union between the chorionic villi with the uterine mucous membrane, that the uterine part of the placenta comes away with the fœtal part at birth. In this case the placenta is either **zonary** (carnivora, pinnipedia, elephant) or discoid (apes, insectivora, edentata, rodentia).

446. CHRONOLOGY OF HUMAN DEVELOPMENT.—**Development during the 1st Month.**—At the 12–13th day the ovum is saccular (5·5 mm. and 3·3 mm. in diameter); there is simply the blastodermic vesicle, with the blastoderm at one part, consisting of two layers; the zona pellucida beset with small villi (*Reichert*). At the **15th–16th day** the ovum (5–6 mm.) is covered with simple cylindrical villi. The zona pellucida consists of embryonic connective-tissue-covered with a layer of flattened epithelium. The **primitive groove** and the **laminæ dorsales** appear. Then follows the stage when the **allantois** is first formed. At the 15th–18th day Coste investigated an ovum. It was 13·2 mm. long, with small branched villi; the embryo itself was 2·2 mm. long, of a curved form, and with a moderately enlarged cephalic end. The amnion, umbilical vesicle with a wide vitelline duct, and the allantois were developed, the last already united to the false amnion. The S-shaped heart lies in the cardiac cavity, shows a cavity and a bulbus aortæ, but neither auricles nor ventricles. The visceral arches and clefts are indicated, but they are not perforated. The omphalo-mesenteric vessels forming the first circulation on the umbilical vesicle are developed, the duct (vitelline) is still quite open, and two primitive aortæ run in front of the protovertebræ. The allantois attached to the fœtal membranes is provided with blood-vessels. The two omphalo-mesenteric veins unite with the two umbilical veins, and pass to the venous end of the heart. The mouth is in process of formation. The limbs and sense-organs absent; the Wolffian bodies probably present.

At the **20th day** all the **visceral arches** are formed, and the clefts are perforated. The mid-brain forms the highest part of the brain, while the two auricles appear in the heart. The connection with the umbilical vesicle is still moderately wide. The embryo is 2·6–3·3–4 mm. long, while the head is turned to one side (*His*). At a slightly later period the temporal and cervical flexures take place, and the hemispheres appear more prominently; the vitelline duct is narrowed, the position of the liver is indicated, while the limbs are still absent (*His*).

At the **21st day** the ovum is 13 mm. long and the embryo 4–4·5 mm.; the umbilical vesicle 2·2 mm., and the intestine almost closed. Three branchial clefts, Wolffian bodies laid down, and the *first appearance of the* **limbs**; three cerebral vesicles, auditory capsules present (*R. Wagner*). Coste also observed, in addition, the nasal pits, eye, the opening for the mouth, with the frontal and superior maxillary processes, the heart with two ventricles and two auricles.

End of the 1st Month.—The embryos of 25–28 days are characterised by the distinctly stalked condition of the umbilical vesicle and the distinct presence of limbs. Size of the ovum, 17·5 mm.; embryo, 8–11 mm.; umbilical vesicle, 4·5 mm., with blood-vessels.

2nd Month.—The embryos of 28–35 days are more elongated, and all the branchial clefts are closed except the first. The allantois has now only three vessels, as the right umbilical vein is obliterated. At the 5th week the nasal pits are united with the angle of the mouth by furrows, which close to form canals at the 6th week (*Toldt*). At 35–42 days the embryo is 1·3–1·1 cm. long, the nasal and oral orifices are separated, the face is flat, the limbs show three divisions, the toes are not so sharply defined as the fingers. The outer ear appears as a low projection at the 7th week. The Wolffian bodies are much reduced in size. Length of body at 7th to 8th week, 1·6–2·1 cm.

End of the 2nd Month.—Ovum, 6½ cm.; villi, 1·3 mm. long; the circulation on the umbilical vesicle has disappeared; embryo, 26 mm. long, and weighs 4 grams. Eyelids and nose present; umbilical cord 8 mm. long, abdominal cavity closed, ossification beginning in the lower jaw, clavicle, ribs, bodies of the vertebræ; sex indistinct, kidneys laid down.

3rd Month.—Ovum as large as a goose's egg; beginning of the placenta; embryo 7–9 cm., weighing 11 grams, and is now spoken of as a **fœtus.** External ear well formed; umbilical cord 7 cm. long. Beginning of the difference between the sexes in the external genitals, umbilicus in the lower fourth of the linea alba.

4th Month.—Fœtus, 17 cm. long, weighing 57 grams, sex distinct; hair and nails beginning to be formed, placenta weighs 80 grams, umbilical cord 19 cm. long, umbilicus above the lowest third of the linea alba; contractions or movements of the limbs; meconium in the intestine; skin with blood-vessels shining through it, eyelids closed.

5th Month.—Fœtus, length of body, 9·7–14·7 cm., total length 18 to 28 cm., weighing 284

grams ; hair on the head and lanugo distinct ; skin still somewhat red and thin, and covered with vernix caseosa (§ 287, 2), is less transparent ; weight of placenta, 178 grams ; umbilical cord, 31 cm. long.

6th Month.—Fœtus, length of body, 9·7–14·7, total length, 18–28 cm., weighing 638 grams ; lanugo more abundant; vernix more abundant ; testicles in the abdomen ; pupillary membrane and eyelashes present ; meconium in the large intestine.

7th Month.—Fœtus, length of body, 18–22·8, total length, 35–38 cm., weighing 1218 grams, the descent of the testicles begins—*one* testicle in the inguinal canal—the eyes open, the pupillary membrane often absorbed at its centre in the 28th week. In the brain other fissures are formed besides the primary ones. The fœtus is capable of living independently. At the beginning of this month there is a centre of ossification in the os calcis.

8th Month.—Fœtus, length of body, 24–27·8, total length 42 cm., weighing 1·5 to 2 kilos. (3·3 to 4·4 lbs.), hair of the head abundant, 1·3 cm. long, nails with a small margin, umbilicus below the middle of the linea alba, one testicle in the scrotum.

9th Month.—Fœtus, length of body, 30–37, total length, 47–67 cm., weighing 2234 grams, and is not distinguishable from the child at the full period.

Fœtus at the Full Period.—Length of body, 51 cm. [20 inches], weight, 3¼ kilos. [7 lbs.], lanugo present only on the shoulders, skin white. The nails of the fingers project beyond the tips of the fingers, umbilicus slightly below the middle of the linea alba. The centre of ossification in the lower epiphysis of the femur is 4 to 8 mm. broad.

Period of Gestation or Incubation (*Schenk*).

	Days.		Days.		Weeks.		Weeks.
Coluber,	12	Rabbit,	} 32	Dog,		Sheep,	21
Hen,	} 21	Hare,		Fox,	} 9	Goat,	22
Duck,			Weeks.	Foumart,		Roe,	24
Goose,	29	Rat,	5	Badger,	} 10	Bear,	} 39
Stork,	42	Guinea-pig,	7	Wolf,		Small apes,	
Cassowary,	65	Cat,	} 8	Lion,	14	Deer,	36–40
Mouse,	24	Marten,		Pig,	17	Woman,	40

Horse, Camel, 13 months ; Rhinoceros, 18 months ; and Elephant, 24 months.

Limitation of the supply of O to eggs, during incubation, leads to the formation of dwarf chicks.

The **movements of the fœtus** can be detected through the abdominal parietes of the mother. They consist in extensor movements of the trunk, movements of the limbs, and toward the end of pregnancy a regular rhythmical movement of the respiratory muscles (*Ahlfeld*) which lasts for some time. Besides these the fœtus makes movements of sucking and swallowing.

447. FORMATION OF THE OSSEOUS SYSTEM.—Vertebral Column.—The ossification of the **vertebræ** begins at the 8th to the 9th week, and first of all there is a centre in each vertebral arch, then a centre is formed in the body behind the chorda, which, however, is composed of two closely apposed centres. At the 5th month the osseous matter has reached the surface, the chorda within the body of the vertebra is compressed ; the three parts unite in the 1st year. The **atlas** has one centre in the anterior arch and two in the posterior ; they unite at the 3rd year. The epistropheus has a centre at the 1st year. The three points of the sacral vertebræ unite or anchylose between the 2nd and the 6th year, and all the vertebræ (sacral) become united to form one body between the 18th and 25th years. Each of the four **coccygeal vertebræ** has a centre from the 1st to 10th year. The vertebræ in later years produce 1 to 2 centres in each process ; 1 to 2 centres in each transverse process ; 1 in the mamillary process of the lumbar vertebræ ; and 1 in each articular process (8 to 15 years). Of the upper and under surfaces of the body of a vertebra each forms an epiphysial thin osseous plate, which may still be visible at the 20th year. Groups of the cells of the chorda are still to be found within the intervertebral discs. As long as the coccygeal vertebræ, the odontoid process, and the base of the skull are cartilaginous, they still contain the remains of the chorda (*H. Müller*). The coccygeal vertebræ form the tail, and they originally project in man like a tail (fig. 811, IX, T), which is ultimately covered over by the growth of the soft parts (*His*).

The **ribs** bud out from the protovertebræ, and are represented on each vertebra. The thoracic ribs become cartilaginous in the 2nd month and grow forwards into the wall of the chest, whereby the seven upper ones are united by a median portion (*Rathke*), which represents the position of one-half of the sternum, and when the two halves meet in the middle line the sternum is formed. When this does not occur we have the condition of the **cleft sternum.** At the 6th month there is a centre of ossification in the manubrium, then 4 to 13 in pairs in the body, and 1 in the ensiform process. Each rib has a centre of ossification in its body at the 2nd month, and at the 8th to 14th one in the tubercle and another in the head. These anchylose at the 14th to 25th year. Sometimes cervical ribs are present in man, and they are largely developed in birds.

The skull.—The chorda extends forwards into the axial part of the base to the sphenoid bone.

The skull at first is **membranous**, or the **primordial cranium**; at the 2nd month the basal portion becomes **cartilaginous**, including the occipital bone, except the upper half, the anterior and posterior part and wings of the sphenoid bone, the petrous part and mastoid process of the temporal bone, the ethmoid with the nasal septum, and the cartilaginous part of the nose. The other parts of the skull remain **membranous**, so that there is a cartilaginous and membranous primordial cranium.

I. The **occipital bone** has a centre of ossification in the basilar part at the 3rd month, and one in the condyloid part and another in the fossa cerebelli, while there are two centres in the membranous cerebral fossæ. The four centres of the body unite during intra-uterine life. All the other parts unite at the 1st to 2nd year.

II. The **post-sphenoid.**—From the 3rd month it has two centres in the sella turcica, two in the sulcus caroticus, two in both great wings, which also form the lamina externa of the pterygoid process, while the non-cartilaginous and previously formed inner lamina arises from the superior maxillary process of the first branchial arch. During the first half of fœtal life these centres unite as far as the great wings; the dorsum sellæ and the clinoid process, as far as the synchondrosis spheno-occipitalis, are still cartilaginous, but they ossify at the 13th year.

III. The **pre-sphenoid** at the 8th month has two centres in the small wings and two in the body. At the 6th month they unite, but cartilage is still found within them even at the 13th year.

IV. The **ethmoid** has a centre in the labyrinth at the 5th month, then in the first year a centre in the central lamina. They unite about the 5th or 6th year.

V. Amongst the **membrane bones** are the inner lamina of the pterygoid process (one centre), the upper half of the tabular plate of the occipital (two points), the parietal bone (one centre in the parietal eminence), the frontal bone (one double centre in the frontal eminence), three small centres in the nasal spine, spina trochlearis and zygomatic process, nasal (one centre), the edges of the parietal bones (one centre), the tympanic ring (one centre), the lachrymal, vomer, and intermaxillary bone.

The **facial bones** are intimately related to the transformations of the *branchial arches* and *branchial clefts* (fig. 819). The median end of the **first branchial arch** projects inwards from each side towards the large oral aperture. It has two processes, the **superior maxillary process** which grows more laterally towards the side of the mouth, and the **inferior maxillary process**, which surrounds the lower margin of the mouth (fig. 811, IX). From above downwards there grows as an elongation of the basis cranii the **frontal process** (*s*), a broad process with a point (*y*) at its lower and outer angle, the inner nasal process. The frontal and the superior maxillary processes (*r*) unite with each other in such a way that the former projects between the two latter. At the same time there is anchylosed with the superior maxillary process the small **external nasal process** (*n*), a prolongation of the lateral part of the skull, and lying above the superior maxillary process. Between the latter and the outer nasal process is a slit leading to the eye (*a*). Thus the mouth is cut off from the nasal apertures which lie above it. But the separation is continued also within the mouth; the superior maxillary process produces the upper jaw, the nasal process, and the intermaxillary process (*Goethe*)—the latter is present in man, but is united to the upper jaw. The **intermaxillary bone**, which in many animals remains as a separate bone (os incisivum), carries the incisor teeth (fig. 822, A). At the 9th week the hard palate is closed, and on it rests the septum of the nose, descending vertically from the frontal process. The lower jaw is formed from the inferior maxillary process. At the circumference of the oral aperture the lips and the alveolar walls are formed. The **tongue** (fig. 822, A *z*) is formed behind the point of the union of the second and third branchial arches (*His*); while, according to Born, it is formed by an intermediate part between the inferior maxillary processes.

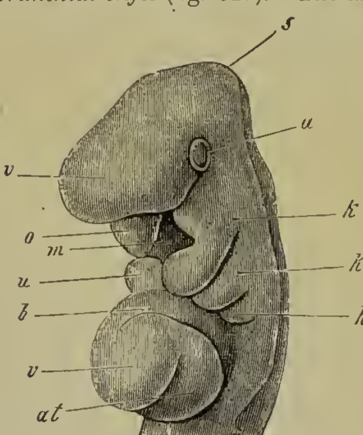


Fig. 819.

Head of embryo rabbit of 10 days (×12). *a*, eye; *at*, atrium or primitive auricle of heart; *b*, aortic bulb; K′, K″, K‴, first (mandibular), second (hyoid), third (1st branchial) visceral arch; *m*, mouth; *s*, superior, and *u*, inferior maxillary process; *s*, mid-brain; *v*, part of head and fore-brain; *v*, ventricle of heart.

Arrested Facial Development.—These transformations may be interrupted. (1) If the frontal process remains separate from the superior maxillary processes, then the mouth is not separated from the nose. This separation may occur only in the soft parts, constituting **hare-lip** (fig. 820); or it may involve the hard palate, constituting **cleft palate.** The hare-lip or cleft palate may occur on both sides. In cleft palate the fissure usually occurs between the incisor teeth. In cases of cleft palate there are often supernumerary incisor teeth.

(2). When there is non-union between the inner and outer nasal process on the one side and the superior maxillary process of the other there is an oblique facial cleft—oro-orbital cleft—(fig. 822, D).

(3). The oral cleft (Makrostomia) may be enormously large laterally and may almost reach the ear (fig. 822, B, *m*).

(4). Extremely seldom is there a fistula of the upper lip.

From the posterior part of the first branchial arch are formed the **malleus** (ossified at the 4th month), and **Meckel's cartilage** (fig. 821), which proceeds from the latter behind the tympanic

Fig. 820.

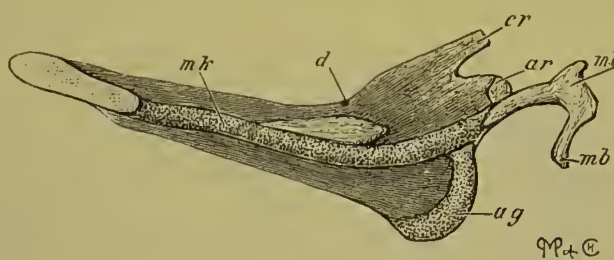


Fig. 821.

Fig. 820.—Hare lip on the left side. Fig. 821.—Inner view of the lower jaw of an embryo pig 3 inches long ($\times 3\frac{1}{2}$). *mk*, Meckel's cartilage; *d*, dentary bone; *cr*, coronoid process; *ar*, articular process (condyle); *ag*, angular process; *ml*, malleus; *mb*, manubrium.

ring as a long cartilaginous process, extending along the inner side of the lower jaw, almost to its middle. It disappears after the 6th month; still its posterior part forms the internal lateral ligament of the maxillary articulation. Near where it leaves the malleus is the processus Folii (*Baumüller*). A part of its median end ossifies, and unites with the lower jaw. The lower jaw is laid down in membrane from the first branchial arch, while the angle and condyle are formed from a cartilaginous process. The union of both bones to form the chin occurs at the first year. From the superior maxillary process are formed the inner lamella of the pterygoid process, the palatine process of the upper jaw, and the palatine bone at the end of the 2nd month, and lastly the malar bone.

The **second arch** [*hyoid*], arising from the temporal bone, and running parallel with the first arch, gives rise to the stapes (although, according to Salensky, this is derived from the first

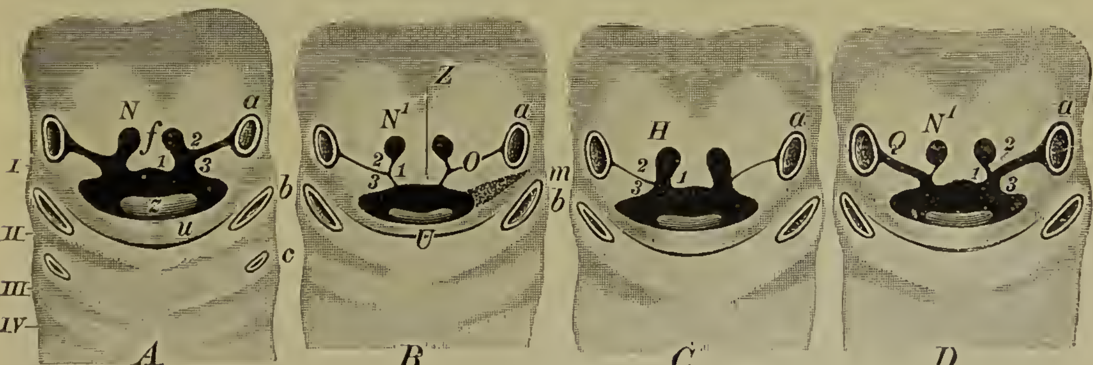


Fig. 822.

Scheme of formation of the face and arrest of its development. A, First appearance of the face; I, II, III, IV, the four visceral arches; *f*, frontal process; 1, inner, and 2, outer nasal processes; 3, superior maxillary process; *u*, inferior maxillary process; *b c*, first and second visceral clefts; *a*, eye; *z*, tongue. B, Normal union of the embryonic parts; Z, intermaxillary bone; N′, nasal orifice; O, nasal tear-duct; U, lower jaw [*m*, abnormal dilation of the mouth, constituting makrostomia]. C, Arrest of the development, constituting oro-nasal cleft. D, Arrest of development showing an "oblique facial cleft" (Q).

arch), the eminentia pyramidalis, with the stapedius muscle, the incus, the styloid process of the temporal bone, the (formerly cartilaginous) stylohyoid ligament, the smaller cornu of the hyoid bone, and lastly the glosso-palatine arch (*His*).

The **third arch** (*thyro-hyoid*) forms the greater cornu and body of the hyoid bone and the pharyngo-palatine arch (*His*).

The fourth arch gives rise to the thyroid cartilage (*His*).

Branchial Clefts.—The first branchial or visceral cleft is represented by the external auditory meatus, the tympanic cavity, and the Eustachian tube; all the other clefts close. Should one or other of the clefts remain open, a condition that is sometimes hereditary in some families, a **cervical fistula** results, and it may be formed either from without or within. Sometimes only a blind diverticulum remains. Branchiogenic tumours and cysts depend upon the branchial arches (*R. Volkmann*).

[**Relation of Branchial Clefts to Nerves.**—It is important to note that the clefts in front of the mouth (pre-oral), and those behind it (post-oral), have a relation to certain nerves. The *lachrymal* slit between the frontal and nasal processes is supplied by the *first division of the trigeminus*. The *nasal slit* between the superior maxillary process and the nasal process is supplied by the bifurcation of the *third nerve*. The *oral cleft*, between the superior maxillary processes and the mandibular arch, is supplied by the *second and third divisions of the trigeminus*. The first post-oral or tympanic-Eustachian cleft, between the mandibular arch (1st) and the hyoid arch, is supplied by the *portio dura*. The next cleft is supplied by the *glosso-pharyngeal*, and the succeeding clefts by branches of the *vagus*.]

The **thymus and thyroid glands** are formed as paired diverticula from the epithelium covering the branchial arches. The epithelium of the last two clefts does not disappear (pig), but proliferates and pushes inwards cylindrical processes, which develop into two epithelial vesicles, the paired commencement of the thyroid glands. These vesicles have at first a central slit, which communicates with the pharynx (*Wölfler*). According to His, the thyroid gland appears as an epithelial vesicle in the region of the 2nd pair of visceral arches in front of the tongue—in man at the 4th week. Solid buds, which ultimately become hollow, are given off from the cavity in the centre of the embryonic thyroid gland. The two glands ultimately unite together. The only epithelial part of the *thymus* which remains is the so-called concentric corpuscles (p. 174). According to Born, this gland is a diverticulum from the 3rd cleft, while His ascribes its origin to the 4th and 5th aortic arches in man at the 4th week. The **carotid gland** is of epithelial origin, being a variety of the thyroid (*Stieda*).

The Extremities.—The origin and course of the nerves of the brachial plexus (§ 355) show that the **upper extremity** was originally placed much nearer to the cranium, while the position of the **posterior extremity** corresponds to the last lumbar and the 3rd or 4th sacral vertebræ (*His*).

The clavicle, according to Bruch, is not a membrane bone, but is formed in cartilage like the furculum of birds (*Gegenbaur*). At the 2nd month it is four times as large as the upper limb; it is the first bone to ossify at the 7th week. At puberty a sternal epiphysis is formed. Episternal bones must be referred to the clavicles (*Götte*). Ruge regards pieces of cartilages existing between the clavicle and the sternum as the analogues of the episternum of animals. The clavicle is absent in many mammals (carnivora); it is very large in flying animals, and in the rabbit is half membranous. The furculum of birds represents the united clavicles.

The scapula at first is united with the clavicle (*Rathke*, *Götte*), and at the end of the 2nd month it has a median centre of ossification, which rapidly extends. Morphologically, the accessory centre in the coracoid process is interesting; the latter also forms the upper part of the articular surface. In birds the corresponding structure forms the **coracoid bone**, and is united with the sternum; while in man only a membranous band stretches from the tip of the coracoid process to the sternum. The long, basal, osseous strip corresponds to the *supra-scapular bone* of many animals. The other centres of ossification are—one in the lower angle, two or three in the acromion, one in the articular surface, and an inconstant one in the spine. Complete consolidation occurs at puberty.

The humerus ossifies at the 8th to the 9th week in its shaft. The other centres are—one in the upper epiphysis, and one in the capitellum (1st year); one in the great tuberosity and one in the small tuberosity (2nd year); two in the condyles (5th to 10th year); one in the trochlea (12th year). The epiphyses unite with the shaft at the 16th to 20th year.

The radius ossifies in the shaft at the 3rd month. The other centres are—one in the lower epiphysis (5th year), one in the upper (6th year), and an inconstant one in the tuberosity, and one in the styloid process. They unite at puberty.

The ulna also ossifies in the shaft at the 3rd month. There is a centre in the lower end (6th year), two in the olecranon (11th to 14th year), and an inconstant one in the coronoid process, and one in the styloid process. They consolidate at puberty.

The carpus is arranged in mammals in two rows. The **first row** contains three bones—the radial, intermediate, and ulnar bones. In man these are represented by the scaphoid, semilunar, and cuneiform bones; the pisiform is only a sesamoid bone in the tendon of the flexor carpi ulnaris. The **second row** really consists of as many bones as there are digits (*e.g.*, salamander). In man the common position of the 4th and 5th fingers is represented by the unciform bone. Morphologically, it is interesting to observe that an os **centrale**, corresponding to the os carpale centrale of reptiles, amphibians, and some mammals, is formed at first, but disappears at the 3rd month, or unites with the scaphoid. Only in very rare cases is it persistent. All the carpal bones are cartilaginous at birth. They ossify as follows:—Os mag-

num, unciform (1st year), cuneiform (3rd year), trapezium, semilunar (5th year), scaphoid (6th year), trapezoid (7th year), and pisiform (12th year).

The metacarpal bones have a centre in their diaphyses at the end of the 3rd month, and so have the **phalanges**. All the phalanges and the first bone of the thumb have their cartilaginous epiphyses at the central end, and the other metacarpal bones at the peripheral end, so that the first bone of the thumb is to be regarded as a phalanx. The epiphyses of the metacarpal bones ossify at the 2nd, and those of the phalanges at the 3rd year. They consolidate at puberty.

The innominate bone, when cartilaginous, consists of two parts—the pubis and the ischium (*Rosenberg*). Ossification begins with **three centres**—one in the ilium (3rd to 4th month), one in the descending ramus of the ischium (4th to 5th month), one in the horizontal ramus of the pubis (5th to 7th month). Between the 6th to the 14th year, three centres are formed where the bodies of the three bones meet in the acetabulum, another in the superficies auricularis, and one in the symphysis. Other accessory centres are :—One in the anterior inferior spine, the crests of the ilium, the tuberosity and the spine of the ischium, the tuberculum pubis, eminentia iliopectinea, and floor of the acetabulum. At first the descending ramus of the pubis and the ascending ramus of the ischium unite at the 7th to 8th year ; the Y-shaped suture in the acetabulum remains until puberty (fig. 823).

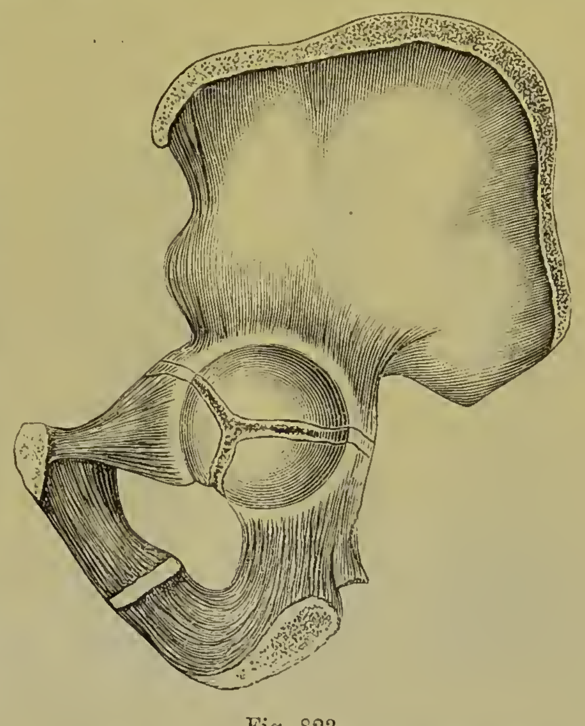


Fig. 823.

Centres of ossification of the innominate bone.

The femur has its middle centre at the end of the 2nd month. At birth, there is a centre in the lower epiphysis ; slightly later in the head. In addition, there is one in the great trochanter (3rd to 11th year), one in the lesser trochanter (13th to 14th year), two in the condyles (4th to 8th year) ; all unite about the time of puberty. The **patella** is a sesamoid bone in the tendon of the quadriceps femoris. It is cartilaginous at the 2nd month, and ossifies from the 1st to the 3rd year.

The tarsus generally resembles the carpus. The os calcis ossifies at the beginning of the 7th month, the astragalus at the beginning of the 8th month, the cuboid at the end of the 10th, the scaphoid (1st to 5th year), the I. and II. cuneiform (3rd year), and the III. cuneiform (4th year). An accessory centre is formed in the heel of the calcaneum at the 5th to 10th year, which consolidates at puberty.

The metatarsal bones are formed like the metacarpals, only later.

[**Histogenesis of Bone.**—The great majority of our bones are laid down in cartilage, or are preceded by a cartilaginous stage, including the bones of the limbs, backbone, base of the skull, sternum, and ribs. These consist of solid masses of hyaline cartilage, covered by a membrane, which is identical with and ultimately becomes the periosteum. The formation of bone, when preceded by cartilage, is called **endochondral bone.** Some bones, such as the tabular bones of the vault of the cranium, the facial bones, and part of the lower jaw, are not preceded by cartilage. In the latter there is merely a membrane present, while from and in it the future bone is formed. It becomes the future periosteum as well. This is called the **intra-membranous** or **periosteal** mode of formation.]

[**Endochondral Formation of Bone.**—(1) The cartilage has the shape of the future bone only in miniature, and it is covered with periosteum. In the cartilage an opaque spot or centre of ossification appears, due to the deposition of lime-salts in its matrix. The cartilage cells proliferate in this area, but the first bone is formed under the periosteum in the shaft, so that an osseous case like a muff surrounds the cartilage. This bone is formed by the sub-periosteal **osteoblasts.** (2) Blood-vessels, accompanied by osteoblasts and connective-tissue, grow into the cartilage from the osteogenic layer of the periosteum (*periosteal processes* of Virchow), so that the cartilage becomes channelled and *vascular*. As these channels extend they open into the already enlarged cartilage lacunæ, absorption of the matrix taking place, while other parts of the cartilaginous matrix become calcified. Thus a series of cavities, bounded by calcified cartilage—the **primary medullary cavities**—are formed. They contain the *primary* or *cartilage*

marrow, consisting of blood-vessels, osteoblasts, and osteoclasts, carried in from the osteogenic layer of the periosteum, and of course the cartilage cells that have been liberated from their lacunæ. (3) The osteoblasts are now in the interior of the cartilage, where they dispose themselves on the calcified cartilage, and secrete or form around them an osseous matrix, thus enclosing the calcified cartilage, while the osteoblasts themselves become embedded in the products of their own activity and remain as **bone-corpuscles.** Bone therefore is at first spongy bone, and as the primary medullary spaces gradually become filled up by new osseous matter it becomes denser, while the calcified cartilage is gradually absorbed. It is to be remembered that, *pari passu* with the deposition of the new bone, bone and cartilage are being absorbed by the **osteoclasts** (fig. 422).]

Chemical Composition of Bone.—**Dry Bone** contains $\frac{1}{3}$ of organic matter or **ossein**, from which gelatin can be extracted by prolonged boiling; and about $\frac{2}{3}$ mineral matter, which consists of neutral calcic phosphate, 57 per cent.; calcic carbonate, 7 per cent.; magnesic

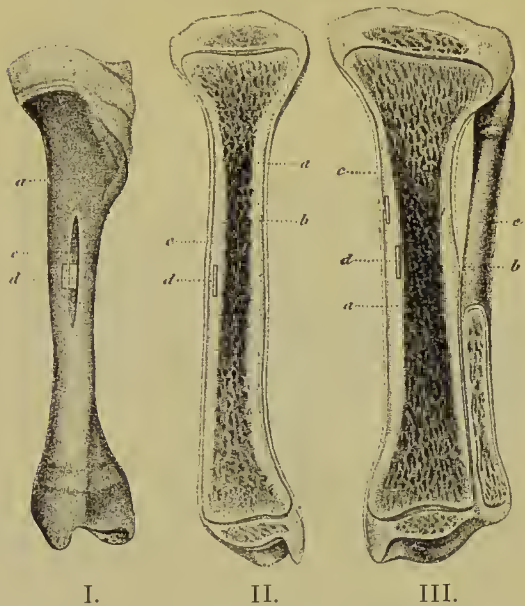


Fig. 824.

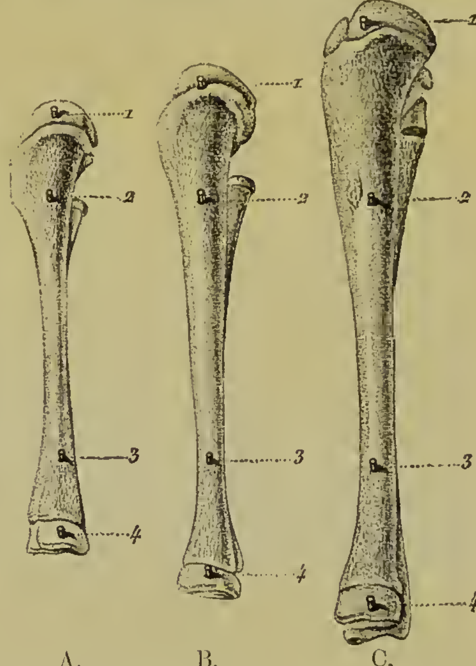


Fig. 825.

Fig. 824.—I, Tibia of a dog. A silver plate (*d*) was inserted under the periosteum, and on the dog being killed after some weeks it was found embedded in the bony shaft at *d* II. III shows a similar bone, where two plates of silver were placed under the periosteum at different times, and after several weeks the one, *d*, was found deeper in the bone than the other. Fig. 825.—Ivory pegs (2 and 3) inserted into the shaft of a growing tibia of a dog. The pegs are still the same distance apart in the adult tibia (*c*), while the pegs 1, 4, inserted in the epiphysis are widely separated in B and C from 2 and 3.

phosphate, 1 to 2 per cent.; calcic fluoride, 1 per cent., with traces of chlorine; and water about 23 per cent. The **marrow** contains fluid fat, albumin, hypoxanthin, cholesterin, and extractives. The *red* marrow contains more iron, corresponding to its larger proportion of hæmoglobin (*Nasse*).

[The **medullary cavity** of a long bone is occupied by *yellow* marrow, which contains about 96 per cent. of fat. The *red* marrow occurs in the ends of long bones, in the flat bones of the skull, and in some short bones. It contains very little fat, and is really lymphoid in its characters, being, in fact, a *blood-forming tissue* (§ 7, C).]

Growth of Bones.—Long bones grow in **thickness** by the deposition of new bone from the periosteum, the osteoblasts becoming embedded in the osseous matrix to form the *bone-corpuscles.* This is proved by inserting a silver plate under the periosteum; after a time bone is formed between the plate and the periosteum, and so the plate comes to lie in the shaft of the bone (fig. 824, *d*). Some of the fibres of the connective-tissue, which are caught up, as it were, in the process, remain as **Sharpey's fibres**, which are calcified fibres of white fibrous tissue, bolting together the peripheric lamellæ. [Müller and Schäfer have shown that there are also fibres in the peripheric lamellæ, comparable to yellow elastic fibres; they branch, stain deeply with magenta, and are best developed in the bones of birds.]

[At the same time that bone is being deposited on the surface, it is being absorbed in the marrow cavity by the action of the **osteoclasts**, so that a metallic ring placed round a bone in a young animal ultimately comes to lie in the medullary cavity (*Duhamel*). The **growth in length** takes place by the continual growth and ossification of the epiphysial cartilage. The cartilage is gradually absorbed from below, but it proliferates at the same time, so that what is lost in one direction is more than made up in the other (*J. Hunter*).]

[The growth in length is shown by placing ivory pegs into a growing bone at a measured distance apart from each other, say 1 and 4 in the epiphysis and 2 and 3 in the shaft (fig. 825). The animals are allowed to live for some months, and then killed, when it is found that the distance between the pegs in the shaft is unchanged (fig. 825, B and C), while the distance between the pegs in the epiphysis and those in the shaft is greatly increased, showing that the bone has grown in length by something intervening between the shaft and epiphysis. This is the **epiphysial cartilage.**]

When the growth of bone is at an end, the epiphysis becomes united to the diaphysis, the epiphysial cartilage itself becoming ossified. It is not definitely proved whether there is an interstitial expansion or growth of the true osseous substance itself, as maintained by Wolff (§ 244, 9).

[**Howship's Lacunæ.**—The **osteoclasts** or myeloplaxes are large multinuclear giant-cells, which erode bone. They can be seen in great numbers lying in small depressions corresponding to them—Howship's lacunæ—on the fang of a temporary tooth, when it is being absorbed. They are readily seen in a microscopical section of spongy bones with the soft parts preserved.]

The **form** of a bone is influenced by external conditions. The bones are stronger the greater the activity of the muscles acting on them. If pressure acting normally upon a bone be removed, the bone develops in the direction of least resistance, and becomes thicker in that direction. Bone develops more slowly on the side of the greatest external pressure, and it is curved by unilateral pressure (*Lesshaft*).

448. DEVELOPMENT OF THE VASCULAR SYSTEM.—Heart.—[The heart appears as a solid mass of cells in the splanchnopleure, at the front end of the embryo, immediately under the "fore-gut." Very soon a cavity appears in this mass of cells; some of the latter float free in the fluid, while the cellular wall begins to pulsate rhythmically. This hollow cellular structure elongates into a tube, which very soon assumes a shape somewhat like an S (fig. 826, 1)] and there are indications of its being subdivided into (*a*) an upper aortic part with the **bulbus arteriosus**; (*b*) a middle or **ventricular part**; and (*v*), a lower venous or **auricular part.** The heart then curves on itself in the form of a horse-shoe (2), so that the venous end (*A*) comes to lie above and slightly behind the arterial end. On the right and left side, respectively, of the venous part is a blind hollow outgrowth, which forms the large auricle on each side (3, *o*, o_1). The flexure of the body of the heart corresponding to the great curvature (2, *V*), is divided into two large compartments (3), the division being indicated by a slight depression on the surface. The large truncus venosus (4, *v*), which joins with the middle of the posterior wall of the auricular part, is composed of the superior and inferior venæ cavæ. This common trunk is absorbed at a later period into the enlarging auricle, and thus arise the separate terminations of the superior and inferior venæ cavæ. In man, the heart soon comes to lie in a special cavity, which in part is bounded by a portion of the diaphragm (*His*). At the 4th to 5th week, the heart begins to be divided into a right and a left half. Corresponding to the position of the vertical ventricular furrow, a septum grows upwards vertically in the anterior of the heart, and divides the ventricular part into a right and left ventricle (5, *R*, *L*). There is a constriction in the heart, between the auricular and ventricular portions, forming the **canalis auricularis.** It contains a communication between the auricle and both ventricles, lying between an anterior and posterior projecting lip of endothelium, from which the auriculo-ventricular valves are formed (*F. Schmidt*). The ventricular septum grows upwards towards the canalis auricularis, and is complete at the 8th week. Thus, the large undivided auricle communicates with the corresponding ventricle by a right and left auriculo-ventricular opening (5). At the same time two septa (4, *p a*) appear in the interior of the **truncus arteriosus** (4, *p*), which ultimately meet, and thus divide this tube into two tubes (5, *ap*), the latter forming the aorta and pulmonary artery, and are disposed towards each other like the tubes in a double-barrelled gun. The septum grows downwards until it meets the ventricular septum (5), so that the right ventricle comes to be connected with the pulmonary artery, and the left with the aorta. The division of the truncus arteriosus, however, takes place only in the first part of its course. The division does not take place above, so that the pulmonary artery and aorta unite in one common trunk above. This communication between the pulmonary artery and the aorta is the **ductus arteriosus Botalli** (7, *B*).

In the **auricle** a septum grows from the front and behind, ending internally with a concave margin. The vena cava superior (6, *Cs*) terminates to the right of this fold, so that its blood will tend to go towards the right ventricle, in the direction of the arrow in 6, *x*. The cava inferior, on the other hand (6, *Ci*), opens directly opposite the fold. On the left of its orifice the valve of the foramen ovale is formed by a fold growing towards the auricular fold, so that

the blood-current from the inferior vena cava goes only to the *left*, in the direction of the arrow, *y*; on the right of the orifice of the cava, and opposite the fold, is the **Eustachian valve**, which, in conjunction with the tubercle of Lower (*tL*), directs the stream from the inferior vena cava to the left into the left auricle, through the pervious **foramen ovale**. Compare the fœtal circulation (§ 445). **After birth**, the valve of the foramen ovale closes that aperture, while the ductus arteriosus also becomes impervious, so that the blood of the pulmonary artery is forced to go through the pulmonary branches proceeding to the expanding lungs. Sometimes the foramen ovale remains pervious, giving rise to serious symptoms after a time, and constituting **morbus ceruleus.**

Arteries.—With the formation of the branchial arches and clefts, the number of aortic arches on each side becomes increased from 1 to 5 (fig. 827), which run above and below each branchial

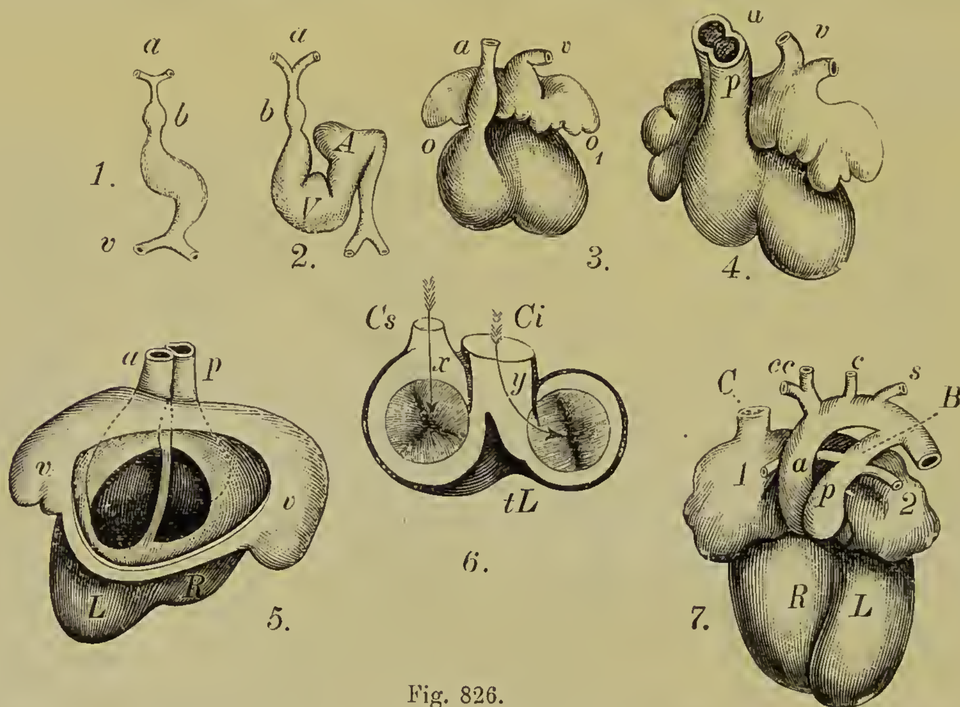


Fig. 826.

Development of the heart. 1, Early appearance of the heart—*a*, aortic part, with the bulbus, *b*; *v*, venous end. 2, Horse-shoe shaped curving of the heart—*a*, aortic end, with the bulbus, *b*; *V*, ventricle; *A*, auricular part. 3, Formation of the auricular appendages, *o*, o_1, and the external furrow in the ventricle. 4, Commencing division of the aorta, *p*, into two tubes, *a*. 5, View from behind of the opened auricle, *v,v*, into the *L*, and *R*, ventricles, and between the two latter the projecting ventricular septum, while the aorta (*a*) and pulmonary artery (*p*) open into their respective ventricles. 6, Relation of the orifices of the superior (*Cs*) and inferior vena cava (*Ci*) to the auricle (schematic view from above)—*x*, direction of the blood of the superior vena cava into the right auricle; *y*, that of the inferior cava to the left auricle; *tL*, tubercle of Lower. 7, Heart of the ripe fœtus—*R*, right, *L*, left ventricle; *a*, aorta, with the innominate, *c,c*, carotid, *c*, and left subclavian artery, *s*; *B*, ductus arteriosus; *p*, pulmonary artery, with the small branches *1* and *2*, to the lungs.

cleft, in a branchial arch, and then all reunite behind in a common descending trunk (2, *ad*) (*Rathke*). These blood-vessels remain only in animals that breathe by gills (fig. 146). In man, the upper two arches disappear completely (3). When the truncus arteriosus divides into the pulmonary artery and the aorta (4, *P*, *A*), the lowest arch on the left side, with its origin, forms the pulmonary artery (4), and it springs from the right side of the heart. Of these the *left* lowest arch forms the **ductus arteriosus** (*dB*), and from the commencement of the latter proceed the pulmonary branches of the pulmonary artery. Of the remaining arches which are united with the aorta, the left middle one (*i.e.*, the fourth left) forms the permanent aortic arch into which the ductus arteriosus opens, while the right one (fourth) forms the subclavian artery; the third arch forms on each side the origin of the carotids (*Ci*, *Cc*). The arteries of the first and second circulations have been referred to already (§ 442). When the umbilical vesicle, with its primary circulation, diminishes, only *one* omphalo-mesenteric artery is present, which gives

a branch to the intestine. At a later period, the omphalo-mesenteric arteries atrophy, while the artery to the intestine—the superior mesenteric—becomes the largest of all, it being originally derived from one of the omphalo-mesenteric arteries.

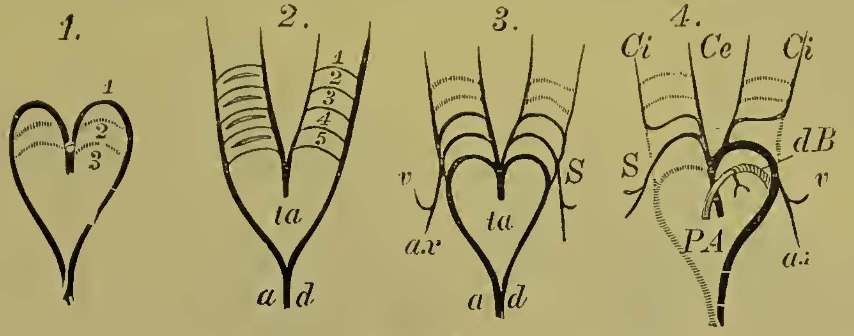


Fig. 827.

The aortic arches. 1. The first position of the 1, 2, and 3 arches. 2. 5 aortic arches ; *ta*, common aortic trunk ; *ad*, descending aorta. 3. Disappearance of the upper two arches on each side—*S*, subclavian artery ; *v*, vertebral artery ; *ax*, axillary artery. 4. Transition to the final stage—*P*, pulmonary artery ; *A*, aorta ; *dB*, ductus arteriosus (*Botalli*) ; *S*, right subclavian, united with the right common carotid, which divides into the internal (*Ci*) and external carotid (*Ce*) ; *ax*, axillary ; *v*, vertebral artery.

Veins of the Body.—The veins first formed in the **body of the embryo** itself are the two **cardinal veins** ; on each side an anterior (fig. 828, I, *cs*), and a posterior (*ci*), which proceed towards the heart and unite on each side to form a large trunk, the **duct of Cuvier** (*DC*), which passes into the venous part of the heart. The anterior cardinal veins give off the subclavian veins (*bb*) and the common jugular veins, which divide into the external (*Ie*) and internal (*Ji*) jugular veins. In addition, there is a *transverse anastomosing branch* passing obliquely from the left (where it divides) to the right, which joins their trunk lower down. In the final arrangement (II) this anastomosis (*As*) becomes very large to form the **left innominate vein**, while with the growth of the arms the subclavian veins increase (*bb*) ; and lastly, the calibre of the jugular vein changes, the internal jugular (*Ji*) becoming very large, and the external jugular (*Ie*) smaller. In some animals, *e.g.*, the dog and rabbit, the large embryonic size is retained. The part of the left superior cardinal vein, from the anastomosis downwards to the left duct of Cuvier, disappears. The **posterior cardinal veins** divide in the pelvis into the hypogastric (I, *h*) and external iliac (*f*, *f*). The inferior cava at first is very small (I, *Vc*), divides at the entrance to the pelvis, and on each side goes into the point of division of the cardinal veins. There is also a transverse ascending anastomosis between the right and left cardinal veins. For the final arrangement, the cava inferior (II, *Ci*) dilates, and with it the hypogastric and external iliac vein on each side. The right cardinal vein remains very small (**Vena azygos**, *Az*), and also the lower part from the left one to the transverse anastomosis. The latter itself also remains very small (*Vena hemiazygos*, *Hz*). On the other hand, the upper part above the anastomosis to the duct of Cuvier disappears. Lastly, the common large venous trunk is so absorbed into the wall of the auricle (*V*) that both venæ cavæ have each a separate orifice (p. 1069). The embryonic condition of the veins persists in fishes (fig. 146, 1).

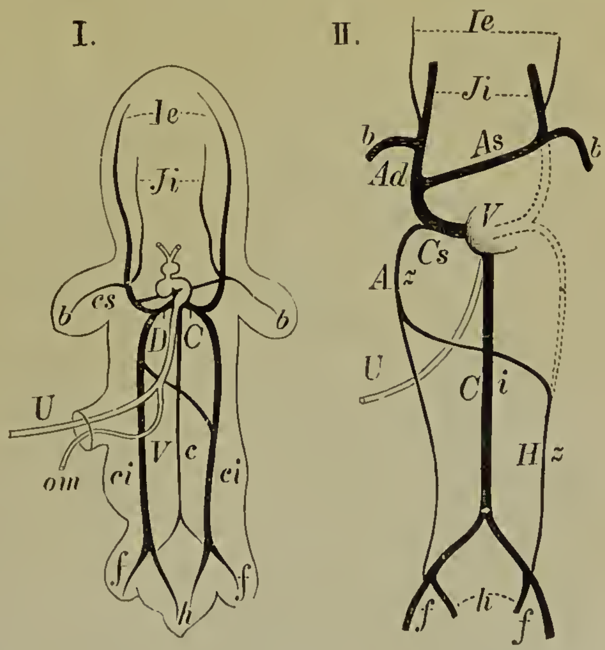


Fig. 828.

I, First appearance of the veins of the embryo. II, Their transformations to form the final arrangement.

Veins of the First and Second Circulation, and Portal System.—The two omphalo-mesenteric veins (om, om_1) open into the posterior or venous end of the tubular heart (fig. 829, 1H). The right vein, however, disappears very soon. As soon as the allantois is formed, the two umbilical veins join the truncus venosus (1, u, u_1). At first the omphalo-mensenteric veins are larger

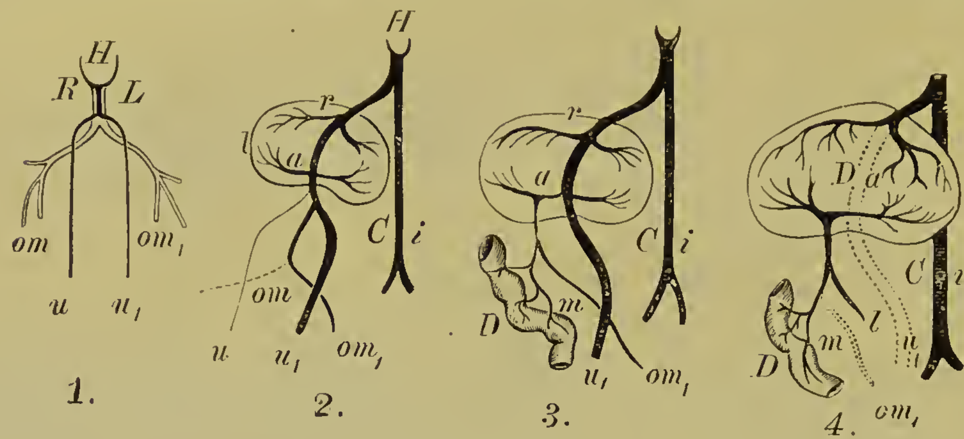


Fig. 829.

Development of the veins and portal system. H, heart; R, L, right and left side of the body; om, right omphalo-mesenteric vein; om_1, left; u, right umbilical vein; u, left; Ci, vena cava inferior; a, venæ advehentes; r, venæ revehentes; D, intestine; m, mesenteric vein; 4, l, splenic vein; 2, l, liver.

than the umbilical veins; at a later period this is reversed, and the right umbilical vein disappears. As soon as veins are formed within the body proper of the embryo, the inferior cava also opens into the truncus venosus (2, Ci). Gradually the umbilical vein (2, u_1) becomes the chief trunk, while the small omphalo-mesenteric (2, om_1) carries little blood.

Portal System.—The umbilical and omphalo-mesenteric veins pass in part directly under the liver to reach the heart. They send branches—carrying arterial blood—to the liver, and the latter grows round these vessels. These branches are the **venæ advehentes** (2 and 3, a). The blood circulating through the liver from the venæ advehentes is returned by other veins, the **venæ revehentes** (2 and 3, r), which reunite at the blunt margin of the liver with the chief trunk of the umbilical vein. The umbilical vein (3, u_1) and the omphalo-mesenteric vein (3, om_1) anastomose in the liver. When the intestine develops (3, D), the mesenteric vein (m) opens into the omphalo-mesenteric vein, and the splenic vein as well (4, l), when the spleen is formed. At a later period, when the omphalo-mesenteric vein (4, om_1) disappears, the vein from the intestine now becomes the common trunk of the previously united vessels. It unites in the liver with the umbilical vein to form the trunk of the vena portæ. When, after birth, the umbilical vein disappears (4, u_1), the mesenteric alone remains as the **portal vein**. As the **ductus venosus** is obliterated, the portal vein must send its blood through the liver, and thus the portal circulation is completed.

449. FORMATION OF THE INTESTINAL CANAL.—The **primitive intestine**, or gut, consists of a straight tube proceeding from the head to the tail. The vitelline duct is inserted at that point, which at a later period corresponds to the lower part of the ileum. At the 4th week the tube makes a slight bend toward the umbilicus (fig. 830, I). As already mentioned, the **vitelline duct** is obliterated, remaining only for a time as a thread attached to the intestine, being still visible at the 3rd month. Sometimes it remains as a short blind tube communicating with the intestine. This is the so-called "*true intestinal diverticulum*"; occasionally a cord—the obliterated omphalo-mesenteric vessels—passes from it to the umbilicus. In very rare cases, the duct may remain open as far as the umbilicus, forming a congenital fistula of the ileum, or it may give rise to cystic formations (*M. Roth*). In a human fœtus at the 4th week, His distinguished the cavity of the mouth, pharynx, œsophagus, stomach, duodenum, mesenterial intestine, and the hind-gut, with the cloaca. The intestine then forms the *first coil* (fig. 830, II) by rotating on itself at the intestinal umbilicus, so that the lower part of the intestine lying next the knee-like bend comes to lie above, while the upper part lies below. From the lower part of this loop there proceed the coils of the **small intestine** (III, t), which gradually grow longer. From the upper limb of the loop, which also elongates, the **large intestine** is formed; first the descending colon, then by elongation the transverse colon, and lastly the ascending colon.

Glands.—By **diverticula**, or protrusions from the intestine, the various glands are formed.

The cells of the hypoblast proliferate and take part in the process, as they form the secretory cells of the glands, while the mesoblastic part of the splanchnopleure forms the membranes of the glands, giving them their shape. The diverticula are as follows :—

1. The **salivary glands**, which grow out from the oral cavity at first as simple solid buds,

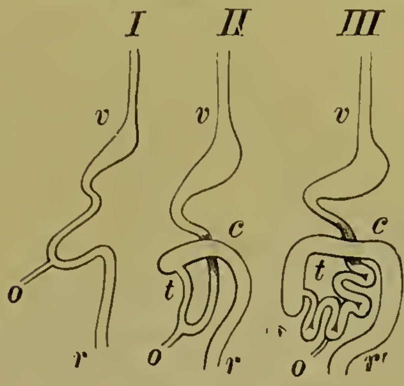


Fig. 830.

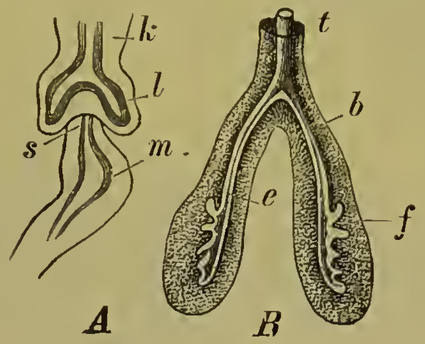


Fig. 831.

Fig. 830.—Development of the intestine. *v*, stomach ; *o*, insertion of the vitelline duct ; *t*, small intestine ; *c*, colon ; *r*, rectum. Fig. 831.—Formation of the lungs. A, Diverticula of the lungs as double sacs—*k*, mesoblastic layer ; *l*, hypoblastic layer ; *m*, stomach ; *s*, œsophagus. B, Further branching of the lungs—*t*, trachea ; *b*, *e*, bronchi ; *f*, projecting vesicles.

but afterwards become hollow and branched. [The salivary glands are developed from the epiblast lining the mouth (stomodæum).]

2. The **lungs**, which arise as two separate hollow buds (fig. 831, A, *l*), and ultimately have only one common duct, are protrusions from the œsophagus. The upper part of the united tracheal tube forms the larynx. The epiglottis and the thyroid cartilage originate from the part which forms the tongue (*Ganghofner*). The two hollow spheres grow and ramify like branched tubular glands with hollow processes (B, *f*). In the first period of development there is no essential difference between the epithelium of the bronchi and that of the primitive air-vesicles (*Stieda*). The **spleen** and **suprarenal capsules**, however, are not developed in this way. The former arises in a fold of the mesogastrium at the 2nd month (*His*) ; the latter are originally larger than the kidneys.

3. The **pancreas** arises in the same way as the salivary glands, but is not visible at the 4th week (*His*).

4. The **liver** begins very early, and appears as a diverticulum, with two hollow **primitive hepatic ducts**, which branch and form bile-ducts. At their periphery they penetrate between the solid masses of cells —the liver-cells — which are derived from the hypoblast. At the 2nd month the liver is a large organ, and secretes at the 3rd month (§ 182).

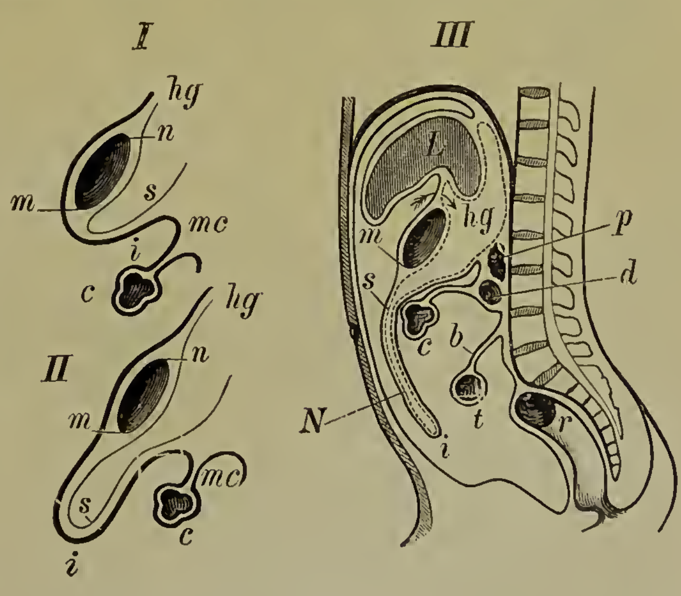


Fig. 832.

Formation of the omentum. I and II, *hg*, gastro-hepatic ligament ; *m*, great, *n*, lesser curvature of the stomach ; *s*, posterior, and *i*, anterior fold or plate of the omentum ; *mc*, mesocolon ; *c*, colon. III, *L*, liver ; *t*, small intestine ; *b*, mesentery ; *p*, pancreas ; *d*, duodenum ; *r*, rectum ; N, great omentum.

5. In birds two small blind sacs are formed from the hind-gut.

6. The fœtal respiratory organ, the **allantois**, is treated of specially (§ 444).

Peritoneum and Mesentery.—The inner surface of the *cœlom*, or body-cavity, the surface of the intestine, and its mesentery are covered by a serous coat—the **peritoneum**. At first the simple intestine is contained in a fold. or duplicature of the peritoneum; on the stomach, which is merely at first a spindle-shaped dilatation of the tube placed vertically, it is called mesogastrium. Afterwards, the stomach turns on its side, so that the left surface is directed forwards and the right backwards. Thus, the insertion of the mesogastrium, which originally was directed backwards (to the vertebral column), is directed to the left; the line of insertion forming the region of the great curvature, which becomes still more curved. From the great curvature, the mesogastrium becomes elongated like a pouch (fig. 832, I and II, *s*, *i*), constituting the omental sac, which extends so far downwards as to pass over the transverse colon and the loops of the small intestine (fig. 832, III, *N*). As the mesogastrium originally consists of two plates, of course the omentum must consist of four plates. At the 4th month, the posterior surface of the omental sac unites with the surface of the transverse colon (*Joh. Müller*).

450. URINARY AND GENERATIVE ORGANS.—Urinary apparatus.—The first indication of this apparatus occurs in the chick at the 2nd day and in the rabbit at the 9th, as the at first solid ducts of the **primitive kidneys** or **Wolffian ducts** (fig. 833, 1, W), which are formed from some cells mapped off from the lateral plate above and to the side of the protovertebræ, and extending from the fifth to the last vertebra. The ducts are solid at first, but soon become hollow, and from their cavities there extend laterally a series of small tubes, which in the chick

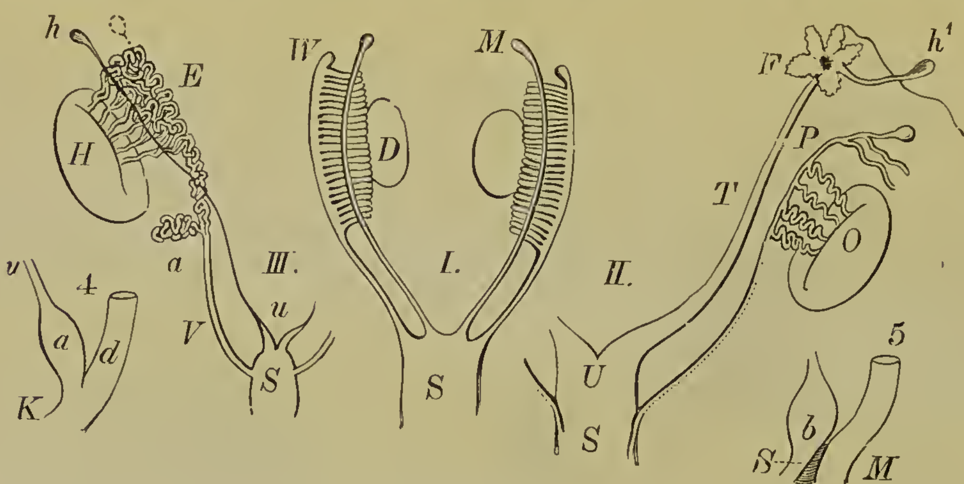


Fig. 833.

Development of the internal generative organs. I., Undifferentiated condition—D, reproductive gland, lying on the tubules of the Wolffian body; W, Wolffian duct; M, Müllerian duct; S, uro-genital sinus. II., Transformations in the female—F, fimbria, with the hydatid, h^1; T, Fallopian tube; U, uterus; S, uro-genital sinus; O, ovary; P, parovarium. III., Transformations in the male—H, testis; E, epididymis, with the hydatid, *h*; *a*, vas aberrans; V, vas deferens; S, uro-genital sinus; *u*, male uterus. 4, *d*, hind-gut; *a*, allantois; *u*, urachus; K, cloaca. 5, M, rectum; *m*, perineum; *b*, position of the bladder; S, uro-genital sinus.

communicate freely with the peritoneal cavity (*Kölliker*). Into one end of each of these tubes grows a tuft of blood-vessels forming a structure resembling the glomeruli of the kidney. The tubes elongate, form convolutions, and increase in number. The upper end of the Wolffian duct is closed at first, its lower end, which lies in a projecting fold—the plica urogenitalis of Waldeyer—in the peritoneal cavity, opens into the uro-genital sinus. Close above the orifice of the Wolffian duct appears the ureter as the duct of the kidney. The duct elongates, and branches at its upper end. Each canal at its end is like a stalked caoutchouc sac (*Toldt*), and into it there grow the already formed glomeruli. The duct of the kidney opens independently into the uro-genital sinus, and forms the **ureter**. The part where the branching of the duct stops forms the pelvis of the kidney, and the branches themselves the renal tubules. Toldt found Malpighian corpuscles in the human kidney at the 2nd month, and Henle's loops at the 4th. The first appearance of the **urinary bladder** is at the 4th week (*His*), and is more distinct at the 2nd month, as the dilated first part of the allantois (fig. 833). The upper part of the allantois remains as the obliterated **urachus**, in the middle vesicle ligament.

Internal Reproductive Organs.—In front of and internal to the Wolffian bodies there arises in the mesoblast the elongated reproductive gland, **germ-ridge**, or mass of **germ-epithelium** (fig. 833, I, D), which in both sexes is originally alike (fig. 834, K, E). In addition, there is

formed a canal or duct parallel to the Wolffian duct (W), which also opens into the uro-genital sinus; this is **Müller's duct** (M). The elevation of the future reproductive gland is covered originally by germ-epithelium (*Waldeyer*). The upper end of the Müllerian duct opens free into the abdominal cavity, while the lower ends of both ducts unite for a distance. Some of the germinal cells covering the surface of the future ovary enlarge to form ova, and sink into the stroma to form ova embedded in their Graafian follicles (§ 433) (fig. 834). In the **female**, the Müllerian ducts form the Fallopian tube (II, T), and the lower united ends the uterus.

In the male, the germ-epithelium is not so tall. According to Waldeyer, there are two kinds of tubes in the Wolffian bodies, and some of these penetrate the position of the reproductive gland. These tubes, which are connected with the Wolffian ducts, become the seminiferous tubules (*v. Wittich*), and the Wolffian duct itself becomes the vas deferens, with the vesiculæ seminales. According to some other observers, however, tubes which become the seminiferous tubules are developed within the reproductive gland itself, and these tubes lined with their germ-epithelium ultimately form a connection with the Wolffian ducts.

The **Müllerian ducts**, which are really the ducts of the reproductive glands, disappear in man, all except the lowest part, which becomes the male uterus or vesicula prostatica (III, *u*)—the homologue of the uterus. The upper tubules of the Wolffian body unite at the 3rd month with the reproductive gland (which has now become the body of the testis), and become the coni vasculosi of the epididymis, which are lined by ciliated epithelium (E); the remainder of the Wolffian body disappears. Some detached tubules form the vasa aberrantia (*a*) of the testicle (*Kobelt*). The hydatid of Morgagni (*h*), at the head of the epididymis, according to Luschka and others, is a part of the epididymis—Fleischl regards it as the rudiment of the male ovary. The organ of Giraldès is part of the Wolffian body. The Wolffian duct itself becomes the vas deferens (V) from which the vesiculæ seminales are developed. The two Wolffian and two Müllerian ducts, as they enter the pelvis, unite to form a common cord—the **genital cord**.

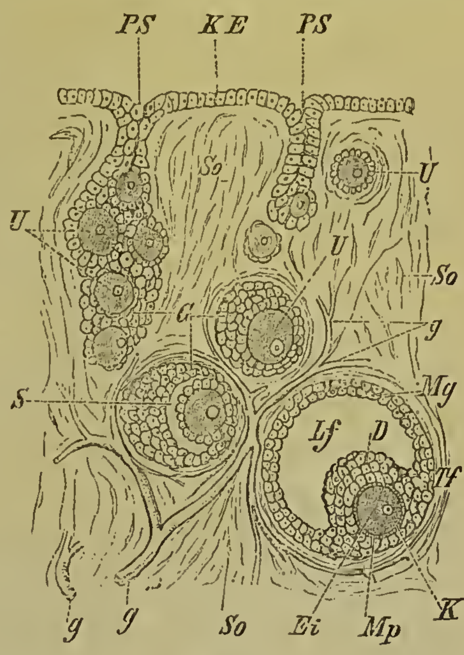


Fig. 834.

Section of mammalian ovary showing development of ova, and their follicles. *Ei*, Ripe ovum; *G*, follicular cells of germinal epithelium; *g*, blood-vessels; *K*, germinal vesicle and spot; *KE*, germinal epithelium; *Lf*, liquor folliculi; *Mg*, membrana granulosa; *Mp*, zona pellucida; *PS*, ingrowths from germinal epithelium, ovarian tubes, by means of which some of the nests retain their connection with the epithelium; *S*, cavity which appears within the Graafian follicle; *So*, stroma of ovary; *Tf*, Theca folliculi or ovi-capsule; *U*, primitive ova.

In the **female**, the tubes of the Wolffian bodies disappear, all except a few tubules, lined with ciliated epithelium, constituting the **parovarium**, or organ of Rosenmüller (fig. 786), and a part analogous to the organ of Giraldès in the broad ligament of the uterus (*Waldeyer*) (fig. 833, P). The same is the case with the Wolffian ducts. In some animals (ruminants, pig, cat, and fox) they remain permanently as the **ducts of Gaertner.**

The Müllerian duct is expanded at its upper end to form the fimbriæ of the Fallopian tube, and it is often provided with a hydatid (h^1). That part of the uro-genital sinus into which the four ducts open grows above into a hollow sphere, which forms the vagina (*Rathke*). According to Thiersch and Leuckart, however, the two Müllerian ducts unite at their lower ends to form the united uterus (U) and vagina, while their free upper ends form the Fallopian tubes (T). The Müllerian ducts at first open into the posterior part of the urinary bladder below the ureters (uro-genital sinus, S), while ultimately this part of the bladder becomes so elongated posteriorly that the vagina (the united Müllerian ducts) and the urethra are united below and deeply within the vestibule of the vagina. At the 3rd to the 4th month, the uterus and vagina are not separate from each other, but at the 5th to the 6th month the uterus is defined from the vagina.

The **testicles** lie originally in the lumbar region of the abdominal cavity (fig. 835, V, *t*), and are carried by a fold of the peritoneum—the mesorchium (*m*). From the hilum of the testicle a cord, the **gubernaculum testis**, runs through the inguinal canal into the base of the scrotum. At the same time a septum-like process is developed independently from the peritoneum to the base of the scrotum (*pr*). The testicle passes through the inguinal canal into the scrotum, but

the mechanism and the cause of the descent are not accurately ascertained.—[Descent of testis, § 446.]

The **ovaries** also descend somewhat. The round ligament of the uterus corresponds to the gubernaculum testis. A process of the peritoneum passes in the female into the inguinal canal as Nuck's canal. It is rare to find the ovaries descending into the labia majora.

[The origin of the urinary and generative organs is undoubtedly associated with the development of the Wolffian bodies. The researches of Semper and Balfour on elasmobranch fishes show that the process is a very complex one. There is a mass of cells on each side of the vertebral column, which is divided into three parts, the first called the **pronephros**, or head-kidney of Balfour and Sedgwick, the middle one, the **mesonephros** or Wolffian body, and the posterior one or **metanephros**, which is formed after the other two, gives origin to the permanent kidney in the amniota. The Müllerian duct is connected with the pronephros, the Wolffian duct with the mesonephros, and the ureter with the metanephros.]

[The following table, modified from Quain, shows the destiny of these structures :—

Female	*Male.*
Müllerian Ducts (Ducts of the Pronephros).	
Fallopian tubes.	Hydatid of Morgagni.
Hydatid.	Male uterus.
Uterus and vagina.	
Wolffian Bodies (Mesonephros).	
Parovarium.	Vasa efferentia, Coni vasculosi.
Paroöphoron.	Organ of Giraldès, Vasa aberrantia.
Round ligament of the uterus.	Gubernaculum testis.
Wolffian Ducts.	
Chief tube of parovarium.	Convoluted tube of epididymis.
Ducts of Gaertner.	Vas deferens and vesiculæ seminales.
Metanephros.	
Kidney.	Ureter.]

The **external genitals** are at first not distinguishable in the two sexes (fig. 835, *I*). At the 14th week there is merely an orifice at the posterior extremity of the trunk, representing both the

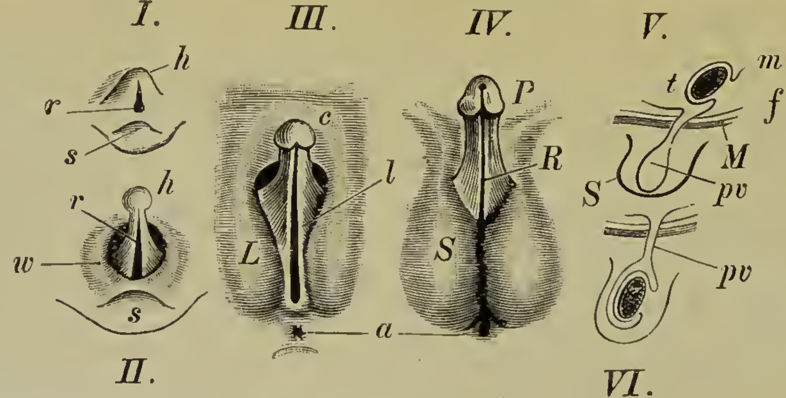


Fig. 835.

Development of the external genitals. *I* and *II*.—Genital eminence ; *r*, genital groove ; *s*, coccyx ; *w*, cutaneous elevations. *IV*.—*P*, penis ; *R*, raphe penis ; *S*, scrotum. *III*.—*c*, clitoris ; *l*, labia minora ; *L*, labia majora ; *a*, anus. *V*. and *VI*.—Descent of the testicle ; *t*, testis ; *m*, mesorchium ; *pv*, processus vaginalis of the peritoneum ; *M*, abdominal wall ; *S*, scrotum.

anus and the opening of the urachus, and forming a **cloaca** (fig. 833, 4, K). In front of this an elevation—the **genital eminence**—appears about the 6th week, and on each side of the orifice a large cutaneous elevation (fig. 835, *II*, *w*). At the end of the 2nd month, there is a groove on the under surface of the genital eminence, leading back to the cloaca, and with distinct walls bounding it (*II*, *r*). At the middle of the 3rd month, the cloacal opening is divided by the growth

of the perineum, between the urachus (now become the urinary bladder) (fig. 833, 5, *b*) and the rectum (*M*).

In the **male**, the genital eminence enlarges, its groove deepens from the opening of the bladder onwards to the apex of the elevation at the 10th week. The two edges unite to enclose the groove, which becomes the urethra. When this does not take place, **hypospadias** occurs. At the 4th month the glans, and at the 6th the prepuce, are formed. The large cutaneous folds meet in the middle line or raphe to form the scrotum.

In the female the undifferentiated condition remains to a certain extent permanent. The small genital eminence remains as the **clitoris**, the margins of its furrow become the **nymphæ**, the cutaneous elevations remain separate to form the **labia majora**. The uro-genital sinus remains short as the vestibulo of the vagina, while in man, by the closing of the genital groove, it has a long additional tube, the urethra. [The accompanying illustrations, after Schroeder, show the changes of the external organs of generation in the female. In the early period (6th week), the hind-gut (fig. 836, R), allantois (ALL), and the Müllerian ducts (M) communicate,

Fig. 836.

Fig. 837.

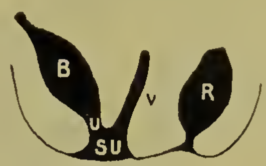


Fig. 838.

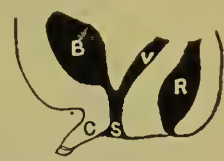


Fig. 839.

Fig. 836.—R, rectum continuous with the allantois (ALL—Bladder); M, duct of Müller (vagina); A, depression of skin below genital eminence, growing inwards to form the vulva. Fig. 837.—The depression has become continuous with the rectum and allantois to form the cloaca (CL). Fig. 838.—The cloaca is becoming divided into uro-genital sinus (SU) and anus by the downward growth of the perineal septum. The ducts of Müller are united to form the vagina (V). Fig. 839.—Perineum completely formed.

but not with the exterior. About the 10th week a depression or inflection of the skin—**genital cleft**—takes place, until it meets the hind-gut and allantois, whereby the cloaca (fig. 837, CL) is formed. The cloaca is then divided into an anterior part, the **uro-genital sinus**, into which the Müllerian ducts open, and a posterior part, the anus. There is a downward growth of the tissue between the hind-gut and the allantois to form the perineum (fig. 838). The uro-genital sinus then contracts at its upper part to form the short urethra, its lower part remaining as the vestibule (fig. 839, SV), while the vagina has been formed by the union of the lower parts of the two Müllerian ducts. The bladder (B) is the expanded lower end of the stalk of the allantois.]

The causes of the difference of sex are by no means well known. From a statistical analysis of 80,000 cases, the influence of the age of the parents has been shown by Kofacker and Sadler. If the husband is younger than the wife, there are as many boys as girls; if both are of the same age, there are 1029 boys to 1000 girls; if the husband is older, 1057 boys to 1000 girls. In insects, food has a most important influence. Pflüger's investigations on frogs show that all external conditions during development are without effect on the determination of the sex, so that the latter would seem to be determined before impregnation.

451. **FORMATION OF THE CENTRAL NERVOUS SYSTEM.**—Fore-brain.—At each side of the fore-brain, or anterior cerebral vesicle, which is covered externally by epiblast and internally by the ependyma, there grows out a large stalked hollow vesicle, the rudiment of the **cerebral hemispheres**. The relatively wide opening in the stalk, or communication, ultimately becomes very small, and is the foramen of Monro. The middle part between the two cerebral vesicles remains small and is the 'tween or **interbrain** with the 3rd ventricle in its interior. It elongates at the second month towards the base of the brain as a funnel-shaped projection, to form the tuber cinereum with the infundibulum. The **thalami optici**, projecting and enlarging from the sides of the 3rd ventricle, narrow the foramen of Monro to a semilunar slit. At the base of the brain are formed, in the 2nd month, the corpora albicantia, at the 3rd the chiasma; while within the 3rd ventricle the commissures are formed. The **hypophysis**, belonging to the mid-brain, is a diverticulum of the nasal mucous membrane, extending through the base of the skull towards the hollow infundibulum, which grows to meet it (fig. 631, *T*). There is, as it were, a tendency to the union of the cavity of the fore-gut with the medullary tube. In the amphioxus (*Kowalewsky*), goose (*Gasser*), and lizard (*Strahl*) the medullary tube communicated originally with the hind-gut by the canalis myeloentericus. The choroid plexus, which grows into the ventricles of the hemispheres through the foramen of Monro, is a vascular development of the ependyma. At the 4th month, the **conarium** (pineal

gland) is formed, and at this time the corpora quadrigemina cover the hemispheres. The **corpora striata** begin to be developed in the cerebral (lateral) ventricle at the 2nd month, while the cornu ammonis is formed at the 4th month. [The external walls and floor of the primitively simple central hemispheres become much thickened, the thickenings in the floor constitute the corpora striata, which protrude into the lateral ventricles, their position being indicated on the surface of the brain by the Sylvian fissure. As they extend backwards, they become connected with the optic thalami (fig. 840, *st, th*). The corpora striata are connected together by the anterior commissure. From the inner wall of each hemisphere, there grow into each lateral ventricle two projections ; the upper one forms the **hippocampus major** or cornu ammonis (fig. 840, *h*), while the lower one becomes folded, remains thin, receives numerous blood-vessels from the falx cerebri, and forms the **choroid plexus** (fig. 840, *pl*).] At the 3rd month, the Sylvian fissure is formed, and the basis of the island of Reil. The permanent cerebral convolutions are formed from the 7th month onwards.

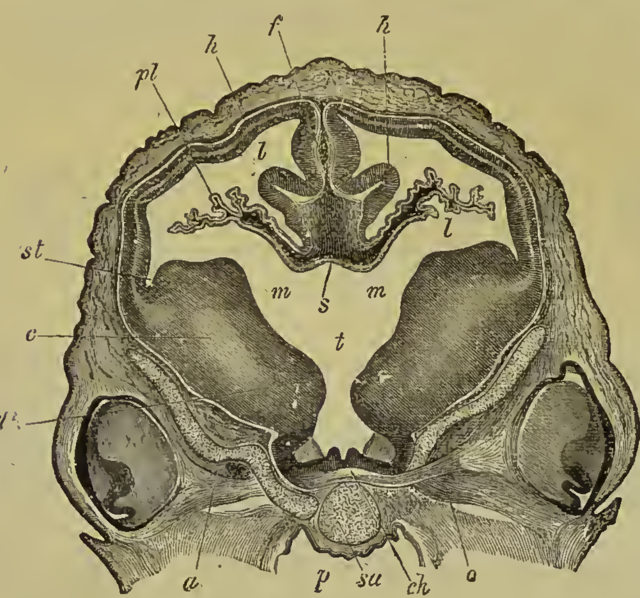


Fig. 840.

Transverse section of the brain of an embryo sheep 2·7 cm. long ; × 10. *a*, cartilage of orbito-sphenoid ; *c*, peduncular fibres ; *ch*, optic chiasma ; *f*, median cerebral fissure ; *h*, cerebral hemispheres, with a convolution upon their inner wall, projecting into the latter ventricle, *l* ; *m*, foramen of Monro ; *o*, optic nerve ; *p*, pharynx ; *pl*, lateral plexus ; *s*, termination of the median fissure, which forms the roof of the third ventricle ; *sa*, body of the anterior sphenoid ; *st*, corpus striatum ; *t*, third ventricle ; *th*, anterior deep portion of the optic thalamus (*Kölliker*).

The **mid-brain**, or middle cerebral vesicle, is gradually covered over by the backward growth of the hemispheres ; its cavity forms the **aqueduct of Sylvius** (fig. 841). Depressions appear on the surface of the vesicle to divide it into four, the **corpora quadrigemina**, in birds into two, the corpora bigemina (fig. 841, *bg*), the longitudinal depression being formed at the 3rd, and the transverse one at the 7th month. The **cerebral peduncle** is formed by a thickening in the base of this vesicle.

In the **hind-brain** are found the cerebellar hemispheres, which grow backwards to meet in the middle line. The vermis is formed at the 7th month. The cerebellum covers in the part of the medullary tube lying below it, which is not closed, as far as the calamus. The **pons** arises in the floor of the hind-brain at the 3rd month.

The spindle - shaped narrow **after-brain** forms the **medulla oblongata**, with the opening of the medullary tube in its upper part.

The following table, from Quain, shows the destiny of each cerebral vesicle :—

I. Anterior Primary Vesicle, . . .	1. *Prosencephalon*, . . . (fore-brain)	Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb.
	2. *Thalamencephalon*, . . (inter or 'tween brain)	Thalami optici, pineal gland, pituitary body, crura cerebri, aqueduct of Sylvius, optic nerve.
II. Middle Primary Vesicle, . . .	3. *Mesencephalon*, . . . (mid-brain)	Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).
III. Posterior Primary Vesicle, . . .	4. *Epencephalon*, ... (hind-brain)	Cerebellum, pons, anterior part of the fourth ventricle.
	5. *Metencephalon*, . . . (after-brain)	Medulla oblongata, fourth ventricle, auditory nerve.

Spinal Cord.—The spinal cord is developed from the medullary tube behind the medulla oblongata, first the grey matter around the canal, while the white matter is added afterwards outside this. The ganglionic cells increase by division in amphibians (*Lominsky*). At first the spinal cord reaches to the coccyx. In the adult, the spinal cord reaches only to the 1st or 2nd

lumbar vertebræ, so that it does not elongate so much as the vertebral canal. It is a question how far this want of harmony in the development of these two structures may lead to disturbances of sensibility or paralysis of the lower limbs in children. The first muscles are formed in the back at the 2nd month; at the 4th month they are red. The **spinal ganglia** are formed from a special strip of epiblastic cells. They are seen at the 4th week, and so are the anterior spinal roots and some of the trunks of the spinal nerves, while the posterior roots are still absent. At this period the ganglia of the 5th, 7th, 8th, 9th, and 10th nerves and part of their origins are present, while the 1st, 2nd, 3rd, and 12th nerves and the sympathetic are not yet far differentiated (*His*). The **motor spinal nerves** grow out from the ganglia-cells of the spinal cord, *i.e.*, from **neuroblasts** (*His*), and penetrate into the peripheral parts of the body (*His*). At first they are devoid of myelin. The cells of the **spinal ganglia** are the parts from which the **sensory nerves** are developed. The nerve-fibres grow into the spinal cord, and there is also a peripheral prolongation towards the skin.

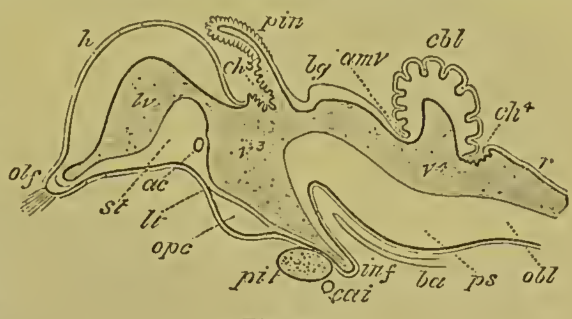


Fig. 841.

Diagram of an embryonic fowl's brain. *ac*, anterior commissure; *amv*, anterior medullary velum, and below it the aqueduct of Sylvius and the cerebral peduncles; *ba*, basilar artery; *bg*, corpora bigemina; *cai*, internal carotid artery; *cbl*, cerebellum; ch^3, ch^4, choroid plexuses of the third and fourth ventricles; *h*, cerebral hemispheres; *inf*, infundibulum; *lt*, lamina terminalis; *lv*, lateral ventricle; *obl*, medulla oblongata; *olf*, olfactory lobe and nerve; *opc*, optic commissure; *pin*, pineal gland; *pit*, pituitary body; *ps*, pons Varolii; *r*, floor of fourth ventricle; *st*, corpus striatum; v^3, third ventricle; v^4, fourth ventricle (*Quain, after Mihalkovics*).

[**Neuroblasts and Spongioblasts.**—When the laminæ dorsales close in the medullary canal (p. 1058) and convert it into the neural canal, they nip off a small part of the epiblast from which is ultimately formed the cerebro-spinal axis. At first the tubular layer consists of one layer of neuro-epithelium, but at a very early stage two kinds of cells are found, one the "**germinal cells**" and the other the "**spongioblasts**" or supporting cells (*His*). The germinal cells lie near the central canal between the inner ends of the spongioblasts (fig. 842), where they form an interrupted row. Each cell has a clear protoplasmic body and the nuclei show mitotic figures. The spongioblasts are columnar palisade-like cells with a radiate arrangement and with oval nuclei lying at some distance from the central canal. The outer ends of these cells give off processes which unite with processes from similar spongioblasts, and this forms the **myelospongium**. From the germinal cells are derived by mitosis the **neuroblasts** (fig. 843), which are pyriform-shaped cells with at first only one process, the axis-cylinder process, which gradually grows out into the anterior nerve-root, so that the fibres of the anterior roots are processes of the neuroblasts, which become the multipolar nerve-cells of the cord. The lateral protoplasmic processes are developed after the axis-cylinder process. The fibres of the posterior root are not developed from their neuroblasts; they are outgrowths of the nerve-cells in the spinal ganglia.]

[**Development of the Sympathetic Nervous System.**—One set of observers (*Balfour*) hold that it is epiblastic in its origin, and another set (*Onodi*) regard it as mesoblastic. Paterson finds that it is of mesoblastic origin, and that it arises on either side of the body as a solid unsegmented rod of cells lying close to the aorta, and at first it has no connections with the cord. It is subsequently connected to the cord by the ingrowth into it of the splanchnic branches of the spinal nerves, and after this connection is made it assumes a segmental appearance.]

452. **THE SENSE ORGANS.**—**Eye.**—The **primary optic vesicle** grows out from the fore-brain towards the outer covering of the head or epiblast, and soon becomes folded in on itself (4th week), so that the stalked optic vesicle is shaped like an egg-cup (fig. 844, I). The cavity in the interior of this cup is called the **secondary optic vesicle**. The inflected part becomes the retina (IV, *r*), while the posterior part becomes the choroidal epithelium (IV, *p*). The stalk becomes the optic nerve. At the under surface of the depression there is a slit—the **choroidal fissure**—which permits some of the mesoblast to gain access to the interior of the eye. This slit forms the **coloboma** (II); it is prolonged backward on the stalk, and contains the central artery of the retina. The margins of the coloboma afterwards unite completely with each other, but in some rare conditions this does not take place, in which case we have to deal with a coloboma of the choroid or retina, as the case may be. In the bird the embryonic coloboma slit does not close up, but a vascular process of the mesoblast dips into it, and passes into the eye to form the **pecten** (§ 405). The same is the case in fishes, where there is a large vascular process of the meso- and epiblast, forming the *processus falciformis* (§ 405).

The depression or inflection of the optic vesicle is due to the downgrowth into it of a

thickening of the epiblast (I, L). It is hollow, and as it grows inwards ultimately becomes spherical and separated from the epiblast to form the **crystalline lens**, so that the lens is epiblastic in its origin, while the capsule of the lens is a cuticular structure formed from the epiblast. That part of the epiblast which covers the vesicle in front of the lens ultimately becomes the stratified epithelium of the cornea. The layer of pigment of the invaginated optic vesicle is applied to the ciliary body, and the posterior surface of the iris, when the latter is formed. The cornea is formed at the 6th week. The substance of the choroid, sclerotic, and cornea is formed around the position of the eye from the mesoblast (*m*). The capsule of the lens is at first completely surrounded by a vascular

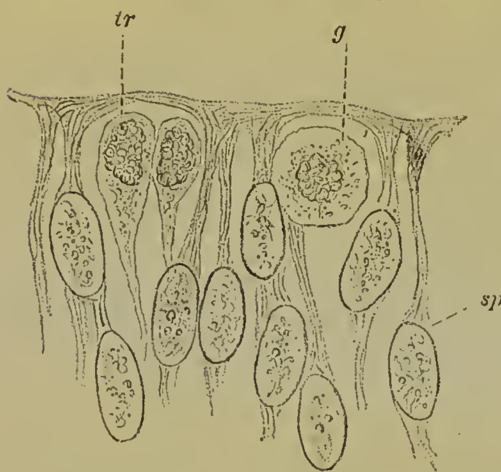


Fig. 842.

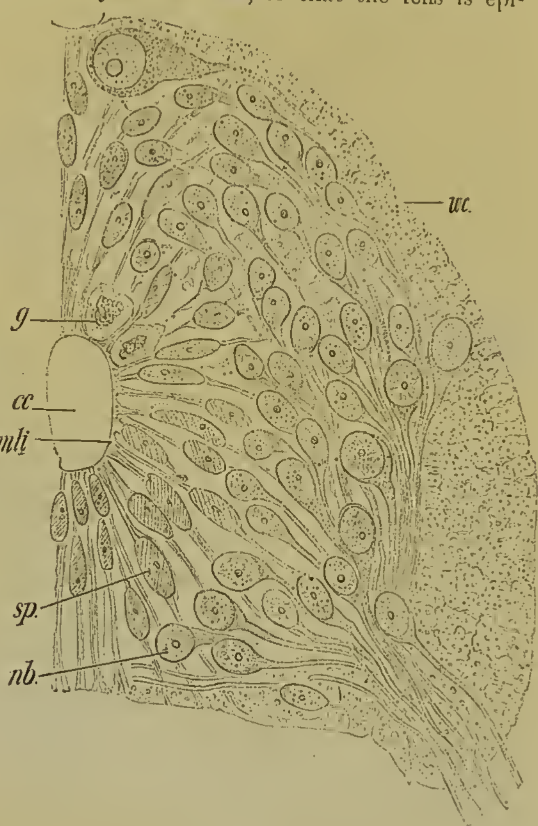


Fig. 843.

Fig. 842.—A group of spongioblasts, *sp*; *g*, germinal cells; *tr*, transition cells between germ-cells and neuroblasts. Fig. 843.—Transverse section of half of the spinal cord of a trout-embryo; *cc*, central canal; *mli*, membrana limitans interna; *g*, germinal cell; *sp*, spongioblast; *nb*, neuroblast; *wc*, white columns.

membrane—the **membrana capsulo-pupillaris**. Afterwards, the lens passes more posteriorly

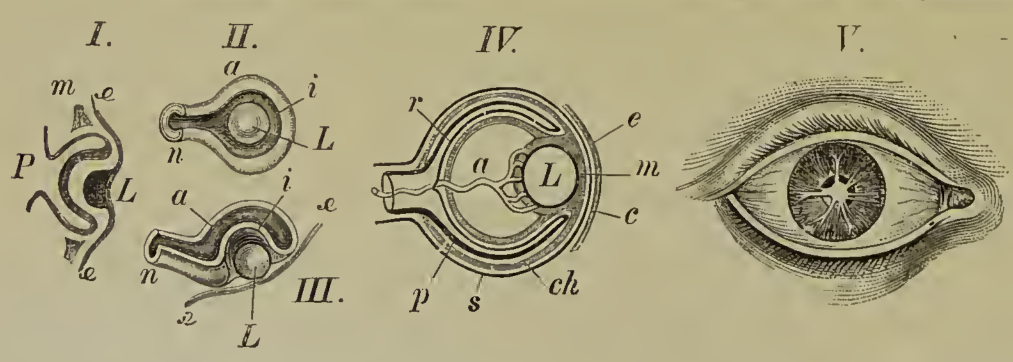


Fig. 844.

Development of the eye. I., Inflexion of the sac of the lens (L) into the primary optic vesicle (P)—*e*, epidermis; *m*, mesoblast. II., The inflexion seen from below—*n*, optic nerve; *e*, the outer, *i*, the inner layer of the inflected vesicle; L, lens. III., Longitudinal section of II. IV., Further development—*e*, corneal epithelium; *c*, cornea; *m*, membrana capsulo-pupillaris; L, lens; *a*, central artery of the retina; *s*, sclerotic; *ch*, choroid; *p*, pigment layer of the retina; *r*, retina. V., Persistent remains of the pupillary membrane.

into the eye—the anterior part of the capsulo-pupillary membrane, however, remains in the anterior part of the eye, while towards it grows the margin of the iris (7th week), so that the

pupil is closed by this part of the vascular capsule, membrana pupillaris. The blood-vessels of the iris are continuous with those of the pupillary membrane; those of the posterior capsule of the lens give off the hyaloid artery, a continuation of the central artery of the retina; its veins pass into those of the iris and choroid. The vitreous humour at the 4th week is represented by a cellular mass between the lens and the retina. The pupillary membrane disappears at the 7th month. It may remain throughout life (V).

Organ of Smell.—On the under surface and lateral limit of the fore-brain, the epiblast forms a groove or pit with thickened epithelium, which forms a depression towards the brain, but always remains as a pit or depression; this is the **olfactory** or **nasal pit**, to which the olfactory nerve afterwards sends its branches. For the formation of the nose, see p. 1072.

Organ of Hearing.—On both sides of the after-brain or posterior brain vesicle, above the first visceral or hyoid arch, there is a depression or pit formed in the epiblast, which gradually

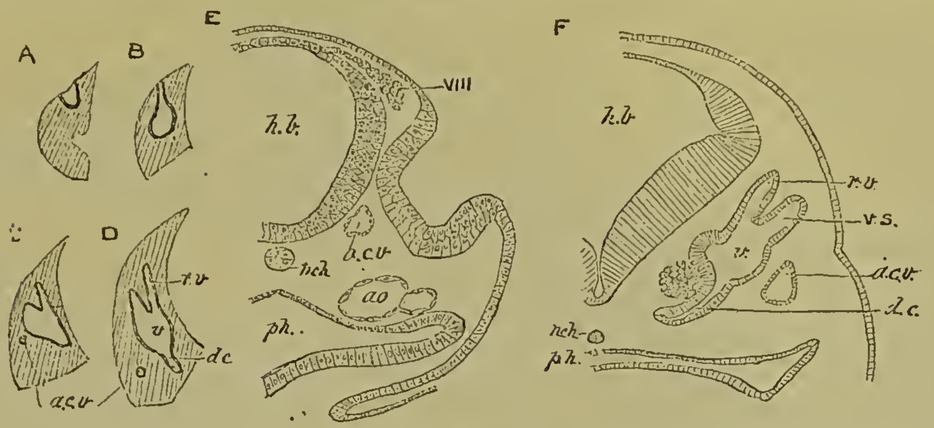


Fig. 845.

Early stages in the development of the vertebrate ear. A–D, early stages in the chick (*Reissner*). E, transverse section through the auditory pit of a 50 hours' chick (*Marshall*). F, transverse section through the hind-brain of a fœtal sheep. *acv*, anterior cardinal (jugular) vein; *ao*, aortic arch; *dc*, ductus cochlearis; *rv*, recessus (aqueductus) vestibuli; *v*, vestibulum; *vs*, vertical semicircular canal; *viii*, auditory nerve; *nch*, notochord.

extends deeper towards the brain—this is the **labyrinth pit** or **auditory sac**, which soon becomes flask-shaped (fig. 845, A, B).

[The stalk, which originally connected the cavity of the sac with the surface, persists as the aqueductus vestibuli; and its blind swollen distal extremity as the **saccus endolymphaticus**, or recessus vestibuli (*Haddon*, fig. 845, *r*, *v*)]. The pit is ultimately completely cut off from the epiblast, just like the lens, and is now called the **vesicle of the labyrinth** or **primary auditory vesicle**. Its related portion forms the utricle, from which, at the 2nd month, the **semicircular canals** and the **cochlea** are developed (fig. 845, D). The union with the brain occurs later, along with the development of the auditory nerve. The first visceral cleft remains as an irregular passage from the Eustachian tube to the external auditory meatus. The *outer ear* appears at the 7th week.

Organ of Taste.—The gustatory papillæ are developed in the later period of intra-uterine life, and several days before birth the taste-buds appear (*Fr. Hermann*).

453. BIRTH.—With the growth of the ovum, the uterus becomes more distended, its walls more muscular and more vascular, although the uterine walls are not thicker at the end of pregnancy. Toward the end of gestation the cervical canal is intact until labour begins, or at any rate it is but slightly opened up at its upper part. After a period of 280 days of gestation, "labour" begins, whereby the contents of the uterus are discharged. The labour pains occur rhythmically and periodically, being separated from each other by intervals free from pain. Each pain begins gradually, reaches a maximum, and then slowly declines. With each pain the heat of the uterus increases (§ 303), while the heart-beat of the fœtus becomes slower and feebler, which is due to stimulation of the vagus in the medulla oblongata (§ 369, 3).

[At the full time the membranes and placenta line the uterus. The membranes consist, from within outwards, of amnion, chorion, decidua reflexa, and decidua

vera. The fundi of the uterine glands persist in the deep part of the decidua vera, and thus form a spongy layer, the part above this being the compact layer in the deep part of the placenta, *e.g.*, near the uterine wall, we have also the fundi of the uterine gland persisting in the decidua serotina. When the placenta and membranes are expelled after birth, the **line of separation** takes place in the part of the membranes and placenta where the fundi of the glands persist. After labour is completely finished, the uterus is lined by the remains of the spongy layer of the decidua vera and serotina, *e.g.*, is lined by a layer which contains the fundi of the uterine glands. The new mucous membrane is **regenerated** by the growth of the epithelium and connective-tissue in this part. The **membranes expelled** are made up of amnion, chorion, deciduæ reflexæ, and the compact layer of the decidua vera.]

The uterine movements during labour proceed in a peristaltic manner from the Fallopian tube to the cervix, and occupy 20 to 30 seconds. In the curve registered by these movements there is usually a more steep ascent than descent.

[**Power in Ordinary Labour.**—Sometimes the ovum is expelled whole, the membranes containing the liquor amnii remaining unruptured. Poppel has pointed out that the force which ruptures the bag of membranes is sufficient to complete delivery, so that, as Matthews Duncan remarks, the strength of the membranes gives us a means of ascertaining the power of labour in the easiest class of natural labours. Matthews Duncan, from experiments on the pressure required to rupture the membranes, concludes that the great majority of labours are completed by a propelling force not exceeding 40 lbs.]

Polaillon estimates the pressure exerted by the uterus upon the fœtus at each pain to be 154 kilos. [338·8 lbs.], so that, according to this calculation, the uterus at each pain performs 8820 kilogrammetres of work (§ 301). [This estimate is certainly far too high.]

After-Birth.—After the fœtus is expelled, the placenta remains behind ; but it is soon expelled by the contractions of the uterus. During the contraction of the uterus to expel the placenta, a not inconsiderable amount of the placental blood is forced into the child (§ 40). [It is more probable that the child aspirates the blood from the fœtus portion of the placenta. This can be seen in late ligature of the cord. The child may thus gain two ounces of blood.] After a time the placenta, the membranes, and the decidua—constituting the **after-birth**—are expelled.

[**Nerves of Uterus.**—The uterus receives its motor fibres for both coats from the sympathetic chain, chiefly from about the 4th to the 6th lumbar ganglia. Most of the fibres run to the lower inferior mesenteric ganglia and are connected with nerve-cells there (*Langley*).]

Influence of Nerves on the Uterus.—1. Stimulation of the hypogastric plexus causes contraction of the uterus. The fibres arise from the spinal cord, from the last dorsal, and upper three or four lumbar nerves, run into the sympathetic and then reach the hypogastric plexus (*Frankenhäuser*). 2. Stimulation of the nervi erigentes, which are derived from the sacral plexus, causes movement (*v. Basch and Hofmann*). 3. Stimulation of the lumbar and sacral parts of the cord causes powerful movements (*Spiegelberg*). There is a *centre for the act of parturition* in the lumbar region of the cord (§ 362, 6). The uterus, like the intestine, probably contains *independent* or *parenchymatous nerve-centres* (*Körner*), which can be excited by suspension of the respiration, and by anæmia (by compressing the aorta, or rapid hæmorrhage). Decrease of the bodily temperature diminishes, while an increase of the temperature increases the movement, which, however, ceases during high fever (*Fromme*). The experiments made by Rein upon bitches show that, if all the nerves going to the uterus be divided, practically all the functions connected with conception, pregnancy, and parturition can take place, even although the uterus is separated from all its cerebro-spinal connections. Hence, we must look to the presence of some **automatic ganglia** in the uterus itself. According to Dembo, there is a centre in the anterior wall of the vagina of the rabbit. According to Jastreboff, the vagina of the rabbit contracts rhythmically. Sclerotic acid greatly excites the uterine contractions (*v. Swiecicki*), so does anæmia (*Kronecker and Jastreboff*). 4. The uterus contracts **reflexly** on stimulating the central end of the sciatic nerve (*v. Basch and Hofmann*), the central end of the branchial plexus (*Schlesinger*), and the nipple (*Scanzoni*). 5. The uterus is supplied by *vaso-motor nerves* (hypogastric plexus), which come from the splanchnic ; and also by *vaso-dilator fibres*, the latter through the nervi erigentes. The vaso-motor nerves are affected reflexly by stimulation of the sciatic nerve (*v. Basch and Hofmann*).

[In the rabbit the vagina and uterine cornua exhibit regular movements of a "peristaltic" nature. These exist apart from any extraneous stimulus, and are probably a vital property of the tissue. They can be demonstrated in animals a few weeks old, and have been recorded continuously for many hours. Frequently they are more vigorous six hours after than at the beginning, showing that they are not due to the irritation of the operation necessary to demonstrate them.

Their rate and extent vary. In young animals they are frequent (1 to 4 per minute) but irregular in character. In nulliparous adults they are less frequent and somewhat more regular. During pregnancy they increase greatly in extent, and their rate becomes 1 in 120 to 130 seconds. These characters are retained after pregnancy for many months at least. They are diminished or abolished by chloroform narcosis, are scarcely affected by ether. Water at 100° to 120° F. produces a persistent contraction accompanied by blanching of the tissue. Similar effects are produced by dilute acetic acid (*Milne Murray*).]

Lochia.—After birth the whole mucous membrane (decidua) is shed; its inner surface, therefore, represents a large wounded surface, on which a new mucous membrane is developed. The discharge given off after birth constitutes the lochia.

Involution of the Uterus.—After birth the thick muscular mass decreases in size, some of its fibres undergoing fatty degeneration. Within the lumen of the blood-vessels of the uterus itself there begins in the interna of these vessels a proliferation of the connective-tissue elements, whereby within a few months the blood-vessels so affected become completely occluded. The smooth muscular fibres of the middle coat of the arteries undergo fatty degeneration. The relatively large vascular spaces in the region of the placenta are filled by blood-clots, which are ultimately traversed by outgrowths of the connective-tissue of the vascular walls.

Milk-Fever.—After birth there is a peculiar action on the vaso-motor system, constituting milk-fever, while at the 2nd to 3rd day there is a more copious supply of blood to the mammary gland for the secretion of milk (§ 231). [After birth the pulse becomes slow and remains so in a normal puerperium. The so-called milk-fever is not found in cases where strict cleanliness is observed during the labour and puerperium.] For the cause of the first respiration in the child, see p. 823.

454. **COMPARATIVE.—HISTORICAL.**—A sketch of the development of man must necessarily have some reference to the general scheme of development in the Animal Kingdom. The question as to how the numerous forms of animal life at present existing on the globe have arisen has been answered in several ways. It has been asserted that each species has retained its characters unchanged from the beginning, so that we speak of the "constancy of species." This view, developed by Linnæus, Cuvier, Agassiz, and others, is opposed by that supported by Lamarck, 1809, or the doctrine of the "Unity of the Animal Kingdom," corresponding to the ancient view of Empedocles, that all species of animals were derived by variations from a few fundamental forms; that at first there were only a few lower forms from which the numerous species were developed—a view supported by Geoffroy St Hilaire and Goethe. After a long period this view was restated and elucidated in the most brilliant and most fruitful manner by Charles Darwin in his "Origin of Species" (1859) and other works. He attempted to show how modifications may be brought about by uniform and varying conditions acting for a long time. Amongst created beings each one struggles with its neighbour, so that there is a real "**struggle for existence.**" Many qualities, such as vigour, rapidity, colour, reproductive activity, &c., are hereditary, so that in this way by "**natural selection**" there may be a gradual improvement, and therewith a gradual change of the species. In addition, organisms can, within certain limits, accommodate themselves to their surroundings or environment. Thus certain useful organs or parts may undergo development while inactive or useless parts may undergo retrogression, and form "**rudimentary organs.**" This process of "natural selection," causing gradual changes in the form of organisms, finds its counterpart in "**artificial selection**" amongst plants and animals. Breeders of animals, for example, by selecting the proper crosses, can within a relatively short time produce very material alterations in the form and characters of the animals which they breed, the changes being more pronounced than many of those that separate well-defined species. But, just as with artificial selection, there is sometimes a sudden "**reversion**" to a former type, so in the development of species by natural selection there is sometimes a condition of **atavism.** Obviously, a wide distribution of one species in different climates must increase the liability to change, as very different conditions of environment come into play. Thus, the migration of organisms may gradually lead to a change of species.

Biological Law.—Without discussing the development of different organisms, we may refer to the "*fundamental biological law*" of Haeckel, viz., "that the ontogeny is a short repetition of the phylogeny," [**ontogeny** being the history of the development of *single* beings, or of the individual from the ovum onwards, while **phylogeny** is the history of the development of a

whole stock of organisms, from the lowest forms of the series upwards] (p. xxvii). When applied to man, this law asserts that the individual stages in the course of the development of the human embryo, *e.g.*, its existence as a unicellular ovum, as a group of cells after complete cleavage, as a blastodermic vesicle, as an organism without a body-cavity, &c.; that these stages of development indicate or represent so many animal forms, through which the human species in the course of untold ages has been gradually evolved. The individual stages which the human race has passed in this process of evolution are rapidly rehearsed in its embryonic development. This conception has not passed without challenge. In any case, the comparison of the human development and its individual organs with the corresponding perfect organs of lower vertebrates is of great importance. Thus, a mammal during the development of its organs is originally possessed of the tubular heart, the branchial clefts, the undeveloped brain, the cartilaginous chorda dorsalis, and many arrangements of the vascular system, &c., which are permanent throughout the life of the lowest vertebrates. These incomplete stages are perfected in the ascending classes of vertebrates. Still, there are many difficulties to contend with in establishing both the evolution hypothesis of Darwin and the biological law of Haeckel.

Historical.—Although the impetus to the study of the history of development has been most stimulated in recent times, the ancient philosophers held distinct but very varied views on the question of development. Passing over the views of Pythagoras (550 B.C.) and Anaxagoras (500 B.C.), Empedocles (473 B.C.) taught that the embryo was nourished through the umbilicus; while he named the chorion and amnion. Hippocrates observed incubated eggs from day to day, noticed that the allantois protruded through the umbilicus, and observed that the chick escaped from the egg on the 20th day. He taught that a 7 months' fœtus was viable, and explained the possibility of superfœtation from the horns of the uterus. The writings of Aristotle (born 384 B.C.) contain many references to development, and many of them are already referred to in the text. He taught that the embryo receives its vascular supply through the umbilical vessels, and that the placenta sucked the blood from the vascular uterus like the rootlets of a tree absorbing moisture. He distinguished the polycotyledonary from the diffuse placenta; and he referred the former to animals without a complete row of teeth in both jaws. In the incubated egg of the chick he distinguished the blood-vessels of the umbilical vesicle, which carried food from the cavity of the latter and also the allantois. He also observed that the head of the chick lay on its right leg, and that the umbilical sac was ultimately absorbed into the body. The formation of double monsters he ascribed to the union of two germs or two embryos lying near each other. During generation the female produces the matter, the male the principle which gives it form and motion. There are also numerous references to reproduction in the lower animals. Erasistratus (304 B.C.) described the embryo as arising by new formations in the ovum—**Epigenesis**,—while his contemporary, Herophilus, found that the pregnant uterus was closed. He was aware of the glandular nature of the prostate, and named the vesiculæ seminalis and the epididymis. Galen (131–203 A.D.) was acquainted with the existence of the foramen ovale, and the course of the blood in the fœtus through it, and through the ductus arteriosus. He was also aware of the physiological relation between the breast and the blood-vessels of the uterus, and he described how the uterus contracted on pressure being applied to it. In the Talmud it is stated that an animal with its uterus extirpated may live, that the pubes separates during birth, and there is a record of a case of Cæsarian section, the child being saved. Sylvius described the value of the foramen ovale; Vesalius (1540) the ovarian follicles; Eustachius († 1570) the ductus arteriosus (Botalli) and the branches of the umbilical vein to the liver. Arantius investigated the duct which bears his name, and he asserted that the umbilical arteries do not anastomose with the maternal vessels in the placenta. In Libavius (1597) it is stated that the child may cry *in utero*. Riolan (1618) was aware of the existence of the corpus Highmorianum testis. Pavius (1657) investigated the position of the testes in the lumbar region of the fœtus. Harvey (1633) stated the fundamental axiom, "*Omne vivum ex ovo.*" Fabricius ab Aquapendente (1600) collected the materials known for the history of the development of the chick. Regner de Graaf described more carefully the follicles which bear his name, and he found a mammalian ovum in the Fallopian tube. Swammerdam († 1685) discovered metamorphosis, and he dissected a butterfly from the chrysalis before the Grand Duke of Tuscany. He described the cleavage of the frog's egg. Malpighi († 1694) gave a good description of the development of the chick with illustrations. Hartsoecker (1730) asserted that the spermatozoa pass into the ovum. The first half of the 18th century was occupied with a discussion as to whether the ovum or the sperm was the more important for the new formation (the Ovulists and Spermatists); and also as to whether the fœtus was formed or developed within the ovum (Epigenesis), or if it merely increased in growth. The question of spontaneous generation has been frequently investigated since the time of Needham in 1745.

New Epoch.—A new epoch began with Caspar Fried. Wolff (1759), who was the first to teach that the embryo was formed from layers, and that the tissues were composed of smaller parts (corresponding to the cells of the present period). He observed exactly the formation of the intestine. William Hunter (1775) described the membranes of the pregnant uterus.

Sœmmering (1799) described the formation of the external human configuration, and Oken and Kieser that of the intestines. Oken and Goethe taught that the skull was composed of vertebræ. Tiedemann described the formation of the brain, and Meckel that of monsters. The basis for the study of the development of an animal from the layers of the embryo was laid by the researches of Pander (1817), Carl Ernst v. Baer (1828–1834), Remak, and many other observers; and Schwann was the first to trace the development of all the tissues from the ovum. [Schleiden enunciated the cell-theory with reference to the minute structure of vegetable tissues, while Schwann applied the theory to the structure of animal tissues. Amongst those whose names are most prominent in connection with the evolution of this theory are Martin Barry, von Mohl, Leydig, Remak, Goodsir, Virchow, Beale, Max Schultze, Brücke, and a host of recent observers.]

APPENDIX A.

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APPENDIX B.

COMPARISON OF THE METRICAL WITH THE COMMON MEASURES.

By Dr Warren De La Rue.

MEASURES OF LENGTH.

	In English Inches.	In English Feet =12 Inches.	In English Yards =3 Feet.
Millimetre	0·03937	0·0032809	0·0010936
Centimetre	0·39371	0·0328090	0·0109363
Decimetre	3·93708	0·3280899	0·1093633
Metre	39·37079	3·2808992	1·0936331
Decametre	393·70790	32·8089920	10·9363310
Hectometre	3937·07900	328·0899200	109·3633100
Kilometre	39370·79000	3280·8992000	1093·6331000
Myriometre	393707·90000	32808·9920000	10936·3310000

1 Inch=2·539954 Centimetres. | 1 Foot= 3·0479449 Decimetres. | 1 Yard=0·91438348 Metre.

MEASURES OF CAPACITY.

	In Cubic Inches.	In Cubic Feet=1,728 Cubic Inches.	In Pints=34·65923 Cubic Inches.
Millilitre or cubic centimetre	0·061027	0·0000353	0·001761
Centilitre or 10 cubic centimetres	0·610271	0·0003532	0·017608
Decilitre or 100 cubic centimetres	6·102705	0·0035317	0·176077
Litre or cubic decimetre	61·027052	0·0353166	1·760773
Decalitre or centistere	610·270515	0·3531658	17·607734
Hectolitre or decistere	6102·705152	3·5316581	176·077341
Kilolitre or stere, or cubic metre	61027·051519	35·3165807	1760·773414
Myriolitie or decastere	610270·515194	353·1658074	17607·734140

1 Cubic Inch=16·3861759 Cubic Centimetres. | 1 Cubic Foot=28·3153119 Cubic Decimetres.
The unit of volume is 1 Cubic Centimetre.

MEASURES OF WEIGHT.

	In English Grains.	In Troy Ounces. =480 Grains.	In Avoirdupois Lbs. =7,000 Grains.
Milligramme	0·015432	0·000032	0·0000022
Centigramme	0·154323	0·000322	0·0000220
Decigramme	1·543235	0·003215	0·0002205
Gramme	15·432349	0·032151	0·0022046
Decagramme	154·323488	0·321507	0·0220462
Hectogramme	1543·234880	3·215073	0·2204621
Kilogramme	15432·348800	32·150727	2·2046213
Myriogramme	154323·488000	321·507267	22·0462126

The unit of mass in the metrical system is 1 Gramme, which is the mass or weight of 1 Cubic Centimetre (1 c.c.) of water at 4° C., *i.e.*, at its temperature of maximum density.

CORRESPONDING DEGREES IN THE FAHRENHEIT AND CENTIGRADE SCALES.

Fahr.	Cent.	Fahr.	Cent.	Fahr.	Cent.	Cent.	Fahr.	Cent.	Fahr.	Cent.	Fahr.
500°	**260°·0**	140°	60°·0	40°	4°·4	**100°**	**212°·0**	**60°**	**140°·0**	**20°**	**68°·0**
450°	232°·2	135°	57°·2	35°	1°·7	98°	208°·4	58°	136°·4	18°	64°·4
400°	204°·4	130°	54°·4	32°	0°·0	96°	204°·8	56°	132°·8	16°	60°·8
350°	176°·7	125°	51°·7	30°	— 1°·1	94°	201°·2	54°	129°·2	14°	57°·2
300°	148°·9	120°	48°·9	25°	— 3°·9	92°	197°·6	52°	125°·6	12°	53°·6
212°	**100°·0**	115°	46°·1	20°	— 6°·7	**90°**	**194°·0**	**50°**	**122°·0**	**10°**	**50°·0**
210°	98°·9	110°	43°·3	15°	— 9°·4	88°	190°·4	48°	118°·4	8°	46°·4
205°	96°·1	105°	40°·5	10°	—12°·2	86°	186°·8	46°	114°·8	6°	42°·8
200°	**93°·3**	**100**	**37°·8**	5°	—15°·0	84°	183°·2	44°	111°·2	4°	39°·2
195°	90°·5	95°	35°·0	**0°**	**—17°·8**	82°	179°·6	42°	107°·6	2°	35°·6
190°	87°·8	90°	32°·2	— 5°	—20°·5	**80°**	**176°·0**	**40°**	**104°·0**	**0°**	**32°·0**
185°	85°·0	85°	29°·4	—10°	—23°·3	78°	172°·4	38°	100°·4	— 2°	28°·4
180°	82°·2	80°	26°·7	—15°	—26°·1	76°	168°·8	36°	96°·8	— 4°	24°·8
175°	79°·4	75°	23°·9	—20°	—28°·9	74°	165°·2	34°	93°·2	— 6°	21°·2
170°	76°·7	70°	21°·1	—25°	—31°·7	72°	161°·6	32°	89°·6	— 8°	17°·6
165°	73°·9	65°	18°·3	—30°	—34°·4	**70°**	**158°·0**	**30°**	**86°·0**	**—10°**	**14°·0**
160°	71°·1	60°	15°·5	—35°	—37°·2	68°	154°·4	28°	82°·4	—12°	10°·4
155°	68°·3	55°	12°·8	—40°	—40°·0	66°	150°·8	26°	78°·8	—14°	6°·8
150°	65°·5	**50°**	**10°·0**	—45°	—42°·8	64°	147°·2	24°	75°·2	—16°	3°·2
145°	62°·8	45°	7°·2	**—50°**	**—45°·6**	62°	143°·6	22°	71°·6	—18°	—0°·4
										—20°	**—4°·0**

To turn C° into F°, multiply by 9, divide by 5, und add 32°.
To turn F° into C°, deduct 32, multiply by 5, and divide by 9.

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